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THE STATUS OF THE THYROID GLAND IN RELATION TO THE DEVELOPMENT OF THE NERVOUS SYSTEM

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Introduction

Although the physical and mental disorders now associated with dysfunction of the thyroid gland were recognised early in history (Iason, 1947) any understanding of their endocrinological basis was long delayed. Present day concepts did not begin to take shape until as recently as the latter part of the last century when T. B. Curling (1850) first drew attention to cases of defective cerebral development in the absence of the thyroid and, following the recognition by Hilton Fagge (1871) of the distinctions between the sporadic and endemic forms of cretinism, Gull (1873) and later Ord (1877) described a "cretinoid state" (myxoedema) arising in the adult. It was not, however, until experimental studies had revealed the striking part played by the thyroid in controlling both the metabolic and maturational processes of the body that cretinism and myxoedema came to be regarded as one and the same disorder originating at different stages of life. The current view that the retarded mental activity of myxoedema is primarily due to a reduced metabolism, whereas the usually more severe mental defects of the cretin are the result of an impairment to central nervous maturation superimposed upon the metabolic disorder, is supported by anatomical evidence. Lotmar (1929, 1933) reported that the brains of cretins were hypoplastic, while Benda (1947) has referred to oedema and vascular changes which, predisposing the tissues to the type of damage characteristic of anorexia or anaemic asphyxia, ultimately lead to severe loss of cells. Somewhat similar findings have been reported by Marie, Trétiakoff & Stumfer (1920) and more recently diffuse cerebral dysfunction has been demonstrated by the electroencephalographic studies of Topper (1951).

Yet another difference between cretinism and myxoedema is to be found in the way in which the mental symptoms react to medication with thyroid hormone. The response of the myxoedematous individual is almost universally satisfactory, but that of the cretin is so variable as to have given rise to the widely accepted belief that the age at which treatment is started and the vigour with which it is pursued are the major factors which determine its success. Means (1948) is categoric on this point when he states: "If cretinism is recognised in the few month's old infant and adequate thyroid treatment started and maintained without omission throughout life, the chance of normal development of the individual is fair, even in the face of totally atrophic thyroid. If on the other hand, treatment is not started until the cretin is a number of years old, or if having been started it is abandoned, the prospect of securing complete normal development by subsequent treatment is very meagre." Similar views have been expressed by Brown, Bronstein & Kraines (1939) who cited differences in early treatment and the initial severity of the glandular dysfunction as the main reasons for the variability of the cretin's response to replacement therapy, but, at the same time, regarded an I.Q. of 70 as a satisfactory attainment in most cases. Likewise, Wilkins & Fleischmann (1941), in discussing the retardation of cerebral development in the cretin, considered that the structural changes observed by Lotmar (1929, 1933) were due to thyroid deficiency and might be prevented by early therapy. Observations consistent with this viewpoint have been reported by Goodkind & Higgins (1941) who, although finding no evidence to suggest that adequacy of treatment determined ultimate mental attainment, yet noted that the I.Q. of children diagnosed as suffering from juvenile myxoedema responded considerably better to medication than did that of cretinous individuals. This consensus of opinion may be summed up in the words of Simpson (1948) who writes: "If treatment has been delayed for some years the only result may be the conversion of a harmless apathetic idiot into a mischievous, truculent, troublesome semi-idiot," implying that the defects of maturation which ensue in the absence or severe deficiency of thyroid hormone are irreversible.

Many workers, on the other hand, have been unable to agree that ultimate mental achievement is contingent upon the mode of treatment.

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Lewis (1937) for instance, as a result of an extensive survey which took into account the fullest available details covering the patient's own and family histories and the age at which treatment was started, concluded that while promptness and adequacy of treatment were important factors, they were not decisive. Cases were described in which, in spite of early and continuous treatment, the subjects had remained grossly defective: yet others in whom treatment had been delayed or sporadic, and who showed marked physical signs of hypo-thyroidism, had I.Q.'s within the normal range. Similar conclusions were drawn by Gesell, Amatruda & Culotta (1936) who considered that the capacity for response was latent but was favoured by early treatment. Others, who likewise have been unable to confirm any positive relationship between treatment and mental capacity include Rolleston (1934), Bruch & McCune (1944) and Radwin, Michelson, Kramer & Berman (1949).

Thyroid therapy, however adequate, cannot be expected to raise the mentality of the cretin above the level determined by the inherent capacity of the brain (Benda, 1947), and while there can be little doubt that the failure of most cretins to achieve normal mental status is due to some permanent defect in cerebral development the origin of the abnormalities which so frequently fail to respond to treatment is open to question. Tredgold (1929) advanced the hypothesis that there are two types of cretin: one in which the essential condition is a primary amentia upon which the hypothyroidism is superimposed; the other in which the hypothyroidism is uncomplicated. It is well known that congenital abnormalities tend to occur in groups rather than singly, and it is possible that the same factor could give rise to functionally unrelated defects in the development of both brain and thyroid. Such a view has been supported by Goodkind & Higgins (1941) but contested by Brown, Bronstein & Kraines (1939) on the ground that frequently no history of amentia is found in the families of cretins not responding to treatment. If further substantiated, however, it would not only help to explain the inconsistencies between mode of treatment and mental attainment described by Lewis (1937) and others, but would also imply that, within the limits imposed by chronic metabolic disorders, the cerebral defects attributable to uncomplicated thyroid deficiency may be regarded as being as reversible in cretinism as they are in myxoedema.

Any attempt to elucidate the problem by recourse to clinical material is plainly fraught with considerable difficulty. As Benda (1947) has pointed out, untreated cretinism is now rare, few infantile cretins come to autopsy, and pathological changes occurring during early development may well have become obscured in the adult. Furthermore, in any study of the ability of replacement therapy to reverse such changes, the picture is complicated by uncertainties centred about the initial diagnosis, the thoroughness with which the patient has applied the prescribed medication, the possible association with other congenital abnormalities, and by the difficulty of following up patients not confined to institutions. The problem would thus seem to be one which is more likely to be solved by an experimental approach and it is therefore surprising how little work has, until recently, been carried out along these lines. Several studies have been made of the changes which occur, as a result of experimental thyroidectomy, in cerebral histology (Isenschmid, 1918), chemical composition and water content of the brain (Hammett, 1927; Weil, 1941); electrical activity of nervous tissue (Horsten & Boeles, 1949; Woodbury, Hurley, Lewis, McArthur, Copeland, Kirschrink & Goodman, 1952) and behaviour (e.g. Rickey, 1925; Brody, 1940, 1942; Burnham & Leonard, 1941; Carlson, 1941), but this work has mostly been undertaken on mature individuals and none has set out expressly to reproduce in experimental animals conditions analagous to those obtaining in the human cretin. Lately, however, some attempt has been made, based largely on the rat, to measure the effects of thyroidectomy during infancy, and of subsequent therapy, on central nervous structure and function. This paper is concerned with an assessment of the results of such experiments.

Experimental Thyroidectomy

The choice of the laboratory rat for such investigations has many advantages. The thyroid gland, judged by its uptake of radioactive iodine, begins to function only four days before birth at which time the nervous system has attained but an elementary stage of differentiation (Tilney, 1933). The animal is hardy and extremely resistant to infection, while the size of litters is large enough to provide adequate littermate controls for operational procedures. It might be expected, therefore, that a comparison of the structure and functional capacity of the brains of rats thyroidectomised shortly after birth with those of normal siblings would pro-

vide an index of the changes, uncomplicated by congenital abnormalities, likely to occur in congenital hypothyroidism in man.

Three methods of thyroidectomy may be used, each having its special advantages and disadvantages. Surgical removal of the gland in new-born rats was first used successfully by Salmon (1936), but the operation is technically difficult, mortality is high, the parathyroid is almost invariably removed at the same time and small remnants of gland may be overlooked, later to hypertrophy. Chemical thyroidectomy involves the daily administration of goitrogenic drugs either in the food or in the water, or by subcutaneous injection. The mode of action of such substances may vary with their constitution, that of the thiourea group being to inhibit the synthesis of thyroid hormone by preventing the oxidation of iodide (Astwood, 1954) and so produce a hyperplastic non-secreting thyroid (MacKenzie & MacKenzie, 1943). This procedure, which was first used on new-born rats by Hughes (1944), tends to be more certain in its effect than surgical thyroidectomy in so far as the activity of accessory thyroid tissue, which may be overlooked during surgery, is equally inhibited (Meyer & Ransom, 1945). Mortality is lower, the degree of hypothyroidism can be controlled by modifying the dosage, the parathyroid is unaffected, and since the drug will pass the placental barrier treatment can be begun in utero by medicating the mother (Goldsmith, Gordon & Charriper, 1945; Barrnett, 1950). Replacement therapy can be instituted simply by discontinuing the treatment. On the other hand, since the drug does not prevent the release of stores of thyroid hormone existing at the time of treatment is started, chemical thyroidectomy is slower to take effect than the surgical procedure and results in the rat are likely to simulate endemic rather than sporadic cretinism in man. There is the further possibility, suggested by differences between surgically and chemically thyroidectomised adult rats in their responess to shock treatment (Woodbury *et al.*, 1952), that goitrogens may be responsible for as yet undiscovered side effects.

The third technique, radiothyroidectomy, introduced by Goldberg & Chaikoff (1949), consists of injecting a suitable dose of radioactive iodine into the new-born rat on the day of birth. This iodine is almost exclusively concentrated in the thyroid gland which is completely destroyed by its radiations. The procedure would thus seem to have most of the advantages and few of the disadvantages of the surgical and chemical methods: its effect is rapid, the parathyroid seems unaffected, any accessory thyroid tissue is eliminated, and provided the dose is adequate there are no remnants of the gland. Mortality is relatively low, but the possibility of side effects as a result of giving so toxic a substance cannot be excluded.

The Cretinoid Rat

(1) General Characteristics

Salmon (1936) and Scow & Simpson (1945) have given detailed accounts of the appearance and general characteristics of the rat surgically thyro-parathyroidectomised at birth and in most essentials their descriptions apply equally well to rats thyroidectomised by the chemical or radio-methods. Growth by body weight, though little affected until 12-15 days old (Eayrs & Taylor, 1951) often reaches a plateau at about three weeks old, but may continue slowly throughout life. The cretinous young cannot, by their physical characteristics, readily be distinguished from their normal littermates for the first 12 days of life, but thereafter marked differences appear. Developmental changes involving the breakdown of epithelia, e.g. opening of the eyes, external auditory meatus and vagina, are retarded, the face remains foreshortened and sparse infantile hair stands out from the body giving the animal a characteristic "powder-puff" appearance. Oxygen consumption is steadily reduced but, as would be expected, the depression in metabolic rate takes place more rapidly after surgical than after chemical thyroidectomy (Meyer & Ransom, 1945). The abdomen is frequently protruberant, an abnormality, attributed by Salmon (1938) to intestinal stasis, which often coincides with an accumulation of gas (Scow & Simpson, 1945). Storage of fat, particularly in the region of the neck, further adds to the rotund appearance of the animal. Skeletal age is retarded, and endochrondal ossification impaired. The span of life would seem to depend to a great extent on the post-weaning care and feeding of the young, and to be enhanced by the presence of even minute remnants of thyroid tissue. Salmon (1936) had no survivors older than 60 days, whereas those of Scow & Simpson (1945) and of Eayrs & Lishman (1955) had exceeded 20 weeks of age at the end of their experiments. The older cretins suffer from respiratory difficulties and can be heard wheezing for some time after they have been disturbed. A contributory, if not the main, cause of this

disability would seem to be hypoplasia of the trachea which is often threadlike and barely patent.

(2) Innate Behaviour

Behaviourally, the cretinous rat is lethargic, making little attempt to either participate in the gambolling activities of its normal littermate, or, for the first 30 days of life at least, to climb up the sides of its cage. Rather do groups of cretins tend to huddle together in a corner. At the same time such rats can be stimulated into remarkable bursts of activity, but if dropped or overstimulated are subject to fits and may remain for a minute or so in the tonic phase.

A series of tests designed to study the maturation of spontaneously-arising behaviour patterns in the cretinoid rat has been carried out by Eayrs & Lishman (1955). The first appearance of the startle response to a sharp auditory stimulus, the righting reflex and the fore-paw placing reaction were all significantly delayed in the hypothyroid animals. The maturation of the suspension reflex, measured in terms of the increase in the duration of clinging to a horizontal bar, was retarded, this retardation being associated with an absence of the climbing movements which characteristically develop in the normal rat. An additional test, designed to measure the rate of inhibition of the reflex after-discharge which follows the application of painful stimuli to the infant rat (Tilney, 1933), showed that the unco-ordinated bodily activity which normally follows such stimulation was controlled at a significantly later age in the cretinous animal. As a whole these findings may be taken to imply that not only is the assembly of the neural mechanisms responsible for simple reflex activity retarded in the hypothyroid rat, but the assumption of the control of higher centres over basic reflex mechanisms is likewise delayed.

The changes in growth, form, and behaviour which characterise the rat made hypothyroid in infancy are thus so similar to those occurring in the human cretin as to encourage the belief that a more detailed study of those features of development which primarily involve the nervous system should facilitate the interpretation of the relationship between thyroid hormone and central nervous maturation. During the last few years work carried out along these lines has yielded information concerning structural changes which arise as a result of uncomplicated thyroid deficiency and has thrown a little light on the problems of (i) the specificity of thyroid hormone as an intermediary in central nervous maturation; (ii) the reversibility of the changes induced by experimental hypothyroidism, and (iii) the extent to which the influence of the thyroid on the nervous system is mediated directly or indirectly,.

Effect of Uncomplicated Thyroid Deficiency on the Development of Nervous Tissues

(1) Histological Studies

Most of the quantitative studies which have been undertaken in this field have been restricted to that region of frontal cortex which is essential for the mediation of the placing reaction (Brooks, 1933), a pattern of behaviour whose maturation is severely retarded in the cretin. An analysis of the histology of this region showed first, that the perikarya of pyramidal neurons occupying the lamina ganglionaris are significantly reduced in size and second, that their density of aggregation is increased as a result of early thyroid deficiency (Eayrs & Taylor, 1951). Although some degree of correlation might be expected between these two observations, the smaller size of the perikarya in the experimental tissues proved inadequate to account altogether for their closer packing, a reduction in the amount of tissue intervening between the perikarya occurring in the tissues of the cretin.

Further investigations have shown that this phenomenon cannot be attributed either to changes in vascularity (Eayrs, 1954) or in the amount of glial tissue (Eayrs & Taylor, 1951). On the other hand, myelination is retarded in the hypothyroid rat (Barrnett, 1949) and probably of greater significance there occurs a marked diminution in the density of the neuropil involving both axons and dendrites (Eayrs, 1955). The former are reduced in number in all except the molecular layers, but not in proportion to their relative densities. The lamina granularis in which the axon network is by no means the most dense, is predominantly affected; in the lamina multiformis which contains the most axons, the decrement is relatively small. Furthermore, although similar numbers of dendrites arise from the perikarya, these processes show a reduction both in length and amount of branching with the result that the decay in density of the dendritic field with distance from the centre of the perikaryon tends to follow a different pattern in the cretin from that in the normal individual. These observations, originally made on chemically thyroidectomised rats, have since been confirmed after radio-thyroidectomy (Eayrs, 1958).

The growth, multiplication, enlargement and myelination of cell processes, although undoubtedly playing a large part, are not necessarily the only factors which regulate the packing density of perikarya. Peters & Flexner (1950), in their studies of the maturation of the frontal cortex of the guinea pig, found that a considerable increase in the spacing of perikarya coincides with a parallel increase in the volume of the extra-cellular water compartment and occurs at a time when relatively few cell processes can be identified. The subsequent decrease in the chloride space corresponds with that stage of development when axons and dendrites are proliferating most rapidly (Flexner & Flexner, 1949). It would thus appear that, during the growth of neuropil, cell processes must extend into a pre-existing extracellular medium or ground substance which they eventually come to replace. Observations on the development of the axon network in the cretinous rat show that, although the closer packing of the perikarya may reflect a reduction in the amount of extracellular space, the replacement of this space by axons is itself retarded (Eayrs, 1955).

(2) Possible Significance of Histological Changes

It is convenient at this point to assess the possible physiological significance of some of these anatomical changes. In the first place, the reduction in the size of the perikarya and in the length and number of their processes strongly suggests that the synthesis of protein is impaired, a conclusion which receives active support both from the enzymological studies of Hamburgh (1955) and from the reduced rate at which methionine is incorporated into the tissues of thyroidectomised rats (Leblond, Everett & Simmons, 1958). Second, the change in the "patterning" of the neuropil may be explained in terms of a reluctance on the part of cell processes to branch. This has been adequately demonstrated in the case of the dendrites and would readily account for the apparently selective effect of thyroid deficiency upon the axon network in the lamina granularis. This layer contains the sensory plexuses derived by multiple branching from thalamic afferent projections and it is therefore consistent that the diminution of neuropil should here be more marked than in the infraganular cortex where afferent and efferent projection fibres, which branch relatively little, predominate (Lorente de No. 1922; von Bonin, 1950). Little is known outside the realm of speculation of the factors which govern branching in neurons, but it seems probable that, in addition to the essential requirement of an adequate protein synthesis within the perikaryon, the phenomenon is the product of an interaction at the cell membrane between the cell and its environment (Weiss, 1949). In hypothyroidism, the changes which occur in the intercellular matrix of subcutaneous tissues (Brewer, 1951) suggest that the ground substance or interstitial fluid of the central nervous system of cretins may be more highly polymerised and hence more viscous than in the normal individual. Such an abnormality arising during the active growth of the cell process could well account for the distortion observed in the growth of neuropil, but the possibility has not yet been tested experimentally.

It is generally accepted that the capacity for central nervous integration depends on the development of neuropil (Conel, 1947) and whether one adopts a connectionist or a statistical view of the mode of functioning of the cerebral cortex it is clear that, as a result of the impairment to branching in the nervous system of the cretin, the possibility of interaction between neurons must be greatly reduced. Indeed, applying the formulae of Uttley (1955) to the data relating to the axon network and dendritic field of the hypothyroid rat, the probability of connection between axons and dendrites is found to be reduced by a factor of about 85 per cent. So dramatic a reduction might well be expected to have profound repercussions in the field of adaptive behaviour, and assuming that the nervous system operates as a conditional probability machine of the type proposed by Sholl & Uttley (1953) it may be predicted that the cretin will respond only to the more dominant features in its environment and while able to learn in some situation will be unable to do so when only minor cues are available. Furthermore, its general reliability will be impaired. It is therefore of no little interest to examine how far such forecasts are borne out in the cortically mediated behaviour of the cretinoid rat.

Two experiments conducted by Eayrs & Lishman (1955) provide evidence on this point. The decorticate rat shows evidence of motor incapacity only when placed in test situations demanding a high degree of co-ordination (Maier, 1935). In an attempt to measure the effect of the cerebral abnormalities observed in hypothyroidism, normal and cretinous rats were trained to run for food along a spar one inch wide. When training was complete, and the rat

would run immediately on being placed at one end of the spar, tests were carried out with a new spar of the same width at the "start" end but tapered to a point at the "reward" end. The poorer motor co-ordination of the cretinous rats was shown by their stumbling on the narrowing spar at a point closer to the start than the normal; but such rats took fewer trials to learn the simple running procedure and whereas the normal rat would hesitate and often retrace its steps on encountering difficulty this was never the case with the cretin which would persist in the completion of the established habit. Such behaviour is entirely consistent with the reduced sensitivity to the environment predicted on the basis of the conditional probability hypothesis. The more rapid learning of so simple a problem may be attributed to an increased rate of habituation and the rat's perserveration to the inadequacy of the stimuli arising from environmental change to break into the "set" mechanisms responsible for an established motor response.

Similar inferences may be drawn from the behaviour of cretinous rats trained to run an elevated spatial T-maze. There was little difference between these and normal individuals in the number of trials required for learning to criterion, but the cretins ran more slowly, required longer on the maze and made significantly more errors than the controls. On the other hand, the time lost per error by the experimental animals was considerably less. This finding was associated with differences in the overt behaviour of the two groups of rat. On coming to the end of a blind the normal rats would stand up and sniff the air in an investigatory manner apparently in an attempt at re-orientation. The cretins on the other hand tended to retrace immediately. Thus, in this more difficult learning situation, the cretin apparently loses the advantage of speedier habituation, while its increased number of errors and inconsequential behaviour at blinds suggest that, in accordance with prediction, it is less able to take advantage on the sensory input. Differences between these results and the effects of thyroidectomy during adult life on maze learning (Rockwell, 1931; Burnham, 1940; Burnham & Leonard, 1941; Carlson, 1941) provide evidence of the influence of a maturational factor.

The Specificity of Thyroid Hormone for Central Nervous Development

The foregoing evidence makes it abundantly clear that thyroid deficiency *per se* is responsible for many changes in central nervous structure which are reflected in behaviour. We may now enquire to what extent such changes occur as a result of some specific relationship between thyroid hormone and cerebral maturation rather than as a general slowing down of bodily growth as a whole.

(1) The Factor of Age

One explanation which could be advanced to account for the cerebral changes in hypothyroidism is that, by reason of an overall retardation in development, the brain of the cretin corresponds with that of a normal but younger animal. In such case it should be possible to establish a "cerebral age" analagous with the reduced "skeletal age" of individuals thyroidectomised (Salmon, 1938; Ziskin, Salmon & Applebaum, 1940; Scow & Simpson, 1945) or hypophysectomised (Walker, Asling, Simpson, Li & Evans, 1952) during infancy, and with this in mind Eayrs & Goodhead (1959) traced the development of the cerebral cortex from birth to maturity using the same criteria of measurement as had earlier been applied to distinguish the cretinous and normal individual. Their findings showed that the percentage of cortical tissue occupied by the perikarya in the normal rat decreases most rapidly between birth and 18 days old, and that, judged by this criterion alone, the cerebral age of 24 days old cretin could be set at about 14 days. On the other hand, the development of the axon network in the granular layer does not follow a course which could account for the apparently selective retardation seen in the cretinous tissues; nor do changes with advancing age in the pattern of decay of the dendritic field show differences comparable with those distinguishing normal and hypothyroid individuals. It seems reasonable to conclude, therefore, that the brain of the cretinous rat is one in which normal growth has been distorted rather than merely retarded.

(2) The Factor of Growth

Reference has already been made to the possibility that an impairment to protein synthesis as a result of maturation or faulty development of the necessary enzyme systems could be a factor underlying the cerebral hypoplasia of the cretinous rat. It is accordingly of interest to examine the extent to which the changes due to hypothyroidism can be simulated by a reduction in protein synthesis effected by alternative means, such as by restricting the dietary intake.

Biel (1939) showed that inanition during the first 23 days of life has a markedly retarding

effect both on somatic and behavioural development, but employed somewhat different criteria of measurement from those in the studies described earlier in relation to maturation in hypothyroidism. Accordingly, Eayrs & Lishman (1955) used the battery of tests previously described to examine the development of automatic behaviour in rats maintained, by underfeeding, at the same body weight as their cretinous littermates. Their results showed that the startle response, righting reflex and placing reaction were retarded in the time of their first appearance, but considerably less so than in the cretin. On the other hand, the performance of the suspension reflex and duration of after-discharge did not differ significantly from that in the controls. The density of the axon network of such animals has been measured by Eayrs & Horn (1955) who found that the fibre count in the infragranular layers of 24 day old rats starved during infancy was similar to that in the cretins.

The available evidence thus suggests that the effects of starvation, and so presumably of an enforced reduction in the synthesis of protein, though similar in trend, are not identical with those of hypothyroidism and would appear on the whole to be less severe. Since, in the histological studies of Eayrs & Horn (1955), the weights of body and brain of the starved animals was reduced to a level considerably less than that of the hypothyroid without corresponding differences in axon density it seems unlikely that the degree of dietary control of the synthesis of protein was inadequate, and it is reasonable to suspect that an over-riding factor is present in hypothyroidism. Unfortunately the histological observations were made before the apparently selective effect of thyroid deficiency on the development of neuropil in the granular layer had been observed and no fibre counts were made in this region. Nor has any measurement been made of any changes in the growth and branching of dendrites which may occur with inanition. These are problems which clearly must be investigated in the future.

(3) Effect of Thyroid Hormone on Normal Maturation

A further method of investigating a specific relationship between the thyroid and central nervous development by studying the effect of giving thyroid hormone to the normal individual. There is ample evidence that this procedure is effective in advancing the processes of maturation in amphibia, and as early as 1912, Gudernatsch showed that feeding thyroid substance to frog tadpoles promoted metamorphosis without normal growth. During this process, as Weiss (1950) has put it, "many new structures and functions arise, while old ones disappear and the nervous system undergoes a thorough remodelling so as to fit the reorganised system." The nature of some of the changes which take place has recently been described by Tusques (1956). It might, therefore, be anticipated that an accelerated maturation would follow the administration of thyroid hormone to normal mammalian species. Tusques (1956) who studied the effects of this procedure in the rat, observed an advance in certain aspects of somatic maturation, notably in the opening of the eye and ear and in the eruption of the teeth, which were not accompanied by any general increase in growth. On the other hand he was unable to show, on the basis of Nissl preparations, that any change had occurred in cortical structure, and noting that cell spacing appeared to be the same in both experimental and control tissues, inferred that no increase had occurred in the growth of cell processes. On the basis of these observations it was concluded that thyroid hormone does not exert any influence upon the developing nervous system of mammals comparable with that seen in amphibia and that the cerebral changes due to hypothyroidism are secondary to the effects of malnutrition. Such an inference would, however, seem to be premature for a number of reasons. In the first place, no quantitative studies have been carried out and it is unlikely that changes in the growth of neuropil can be adequately assessed on the basis of a subjective judgment of differences in cell spacings in Nissl stained preparations. Secondly, readily observable morphological and histological changes do occur in the cerebellar cortex together with an acceleration in the development of posture and of cage-exploring activities which can only be interpreted as reflecting some maturational change within the central nervous system. Finally, although such very frequently turns out to be the case within set limits, there would appear to be a little justification for presuming that, because of a deficiency of a substance has certain sequelae, a surplus will necessarily produce the opposite effect.

(4) Amelioration of the Effects of Thyroid Deficiency

The ability of substances other than thyroid

hormone to rectify the effects of hypothyroidism might be expected to provide a measure of the specificity of thyroid secretions as an intermediary in cerebral maturation. Accordingly experiments have recently been carried out to determine the extent to which hormones known to have an anabolic influence on protein metabolism can restore the developmental abnormalities resulting from thyroid deficiency (Eayrs, 1959). In addition, the possible ameliorating influence of Vitamin A has been examined (Eayrs, 1956).

(a) Effect of Steroid Anabolists

Testosterone has long been known to stimulate protein anabolism and recently a number of synthetic derivatives has been developed which are claimed to have nitrogen-retaining properties similar to those of testosterone, but without any marked and, from the clinical point of view, undesirable androgenic side-effects. One of these, methylandrostenediol (MAD) was first shown to possess anabolic activity comparable with that of testosterone by Gordan, Eisenberg, Moon & Sakamoto (1951), a finding since confirmed by McSwiney & Prunty (1957) in man and by Korner & Young (1955a) in the rat. A second, 19-nortestosterone has been shown by McSwiney & Prunty (1957) to cause marked nitrogen retention in man although with definite androgenic side-effects.

Both these substances have been tested for their ability to restore protein synthesis in the brain of the hypothyroid rat, but when given to newborn animals, neither has shown any ability to increase growth, and in fact the weights of both body and brain of the treated aniaals were slightly less than those of thyroidectomised controls. Nor did these steroids have any effect on the maturation of the cerebral cortex as measured either by the emergence of the placing reaction or by histological criteria. These findings are unexpected in the light of the observations of Salgado & Selye (1954) who showed that MAD was able completely to restore the bodily growth of thyroidectomised rats, although the effect of its chronic administration to normal animals was eventually deleterious.

It seems possible that one of the factors responsible for the failure of these substances to stimulate growth is that of age, for Korner & Young (1955b) have found that the response of six-month-old rats to the administration of MAD is markedly less than that of rats aged three and a half months. Salgado & Selye do not give the ages of the rats used but judged by their body weight these were post-pubertal at the time of treatment. It appears therefore, that in infant rats the mechanism of response to stimulation of growth by steroid hormones is either deficient or inhibited though there is no evidence at present available to show why this should be. The finding would not appear to apply to all steroids, however, for Parmer (1947) found that deoxycorticosterone acetate would hasten the development of normal newborn rats while being without marked effect on thiouracil-induced cretins. Similar observations in relation to normal rats were made by Mulinos & Pomerantz (1942).

(b) Effect of Pituitary Growth Hormone

Anterior pituitary extracts and purified growth hormone have long been known not only to restore the growth of hypophysectomised rats but also to promote gigantism when chronically administered to normal individuals. Anterior pituitary extract or growth hormone given to rats surgically thyroidectomised after weaning will prevent dwarfing (Flower & Evans, 1952; Smith, 1933) and may even result in abnormally large animals (Evans, Simpson & Pencharz, 1939). There would, however, seem to be disagreement about the efficacy of this treatment in rats thyroidectomised at birth, for Salmon (1938, 1941) failed to obtain any response from such animals following the administration of anterior pituitary implants or growth hormone unless fragments of thyroid tissue were present. On the other hand, others have found that, when treated with growth hormone from 32 days old, thyroidectomised rats gain considerably more weight than their untreated controls (Scow & Marx, 1945) but that the effect is greatly enhanced when doses of thyroxine are given at the same time (Scow, Simpson, Asling, Li & Evans, 1949; Ray, Simpson, Li, Asling & Evans, 1950). Successful treatment of cretinism in man has been recorded following the administration of anterior pituitary extract where thyroxine failed (Rudolf, 1938), and Zamenhof (1942) has reported remarkable changes in the cerebral development of normal rats treated with growth hormone *in utero*.

Recent observations (Eayrs, 1959) have shown that the growth of the normal rat is remarkably little affected by growth hormone given during the first days of life, although a small but significant increase occurred in the weight of the brain. The effect on the growth of both body and brain of the thyroidectomised

rats was on the other hand much more marked. No trace of thyroid tissue was found in any of the experimental animals, and the relative influence of growth hormone on normal and thyroidectomised rats at this very early age would thus seem to be the reverse of that which succeeds treatment begun after weaning. Greater importance, however, attaches to the effect of growth hormone on cortical maturation. Quantitative estimates of cortical structure failed to reveal any significant effect on the density of the axon network in either normal or thyroidectomised animals, but on the other hand in the tissues of both athyroid and normal rats, the dendrites were longer and branched more frequently, these two factors combining to produce dendritic fields of increased density at all distance from the perikaryon. This increase in density and so presumably in cortical connectivity, was associated with an advance in the time at which the placing reaction appeared in both normal and athyroid rats. It is of interest therefore that the administration of growth hormone *in utero* (Zamenhof, 1942) which by contrast results in an increase in cell population rather than of neuropil, does not result in any increased capacity for adaptive behaviour (Warden, Ross & Zamenhof, 1942).

(c) Effect of Giving Vitamin A

The metabolism of thyroid hormone and of Vitamin A and its precursors are closely linked and, for reasons whose discussion is more conveniently deferred until a later section, an investigation has been made of its capacity to counter the effects of early thyroid deficiency (Eayrs, 1956).

As a result of giving daily injection of the vitamin to chemically thyroidectomised rats the weights of both body and brain were significantly increased, the emergence of the placing reflex was advanced and there was a restoration of both the axonal and dendritic components of the neuropil towards the normal pattern and density. In the absence of any evidence that the amelioration was indirectly mediated through changes in bony growth it was suggested that the effects might be due to a direct action of the vitamin on the nervous system for which there are already precedents (Millen, Woollam & Lamming, (1953). Attempts to repeat these results, however, using radio-thyroidectomised animals, have not met with success so that it now seems possible that the improvement in cerebral maturation may have been due to an antagonising effect of the vitamin upon the action of methyl thiouracil, the goitrogen used.

The Reversibility of the Effects of Cretinism

The experiments just described have investigated the ability of various substances to prevent the changes characteristic of early hypothyroidism. It remains to consider how far such defects, once they have been allowed to develop can be rectified by measures applied later in life. Only one therapeutic agent, thyroxine, has so far been examined in this respect the available evidence being based on studies of cortical histology, adaptive behaviour and enzymology.

(1) Histological Evidence

Lishman (1953) and Horn (1955) have examined the effect of giving thyroxine to rats radio-thyroidectomised at birth, treatment being started on the sixth day of life. The latter measured the density of the axon network in the visual cortex at 60 days old and found that, while the fibre count in the laminae pyramidalis and ganglionaris was not fully restored to normal after 36 days of medication, comparison with the condition in the untreated cretin showed that a good measure of recovery had occurred. Lishman (1953) found that the fibre count in all cortical layers had been fully restored to normal after 23 weeks of treatment while the density in untreated cretins of the same age still fell far short of normal. It would thus seem that, judged by this limited histological evidence at least some of the effects of thyroid deficiency arising during the first 24 days of life in the rat are not irreversible.

(2) Evidence from Behavioural Studies

Eayrs & Lishman (1955) found that the performance of thyroxine-medicated cretins on an elevated T-maze was in every way as good as that of normal controls. These results thus conform with the histological evidence. Such animals on the other hand proved inferior to their controls in solving the three-table problem introduced by Maier (1932) as a test of "reasoning". This suggests that the reversibility of the effects of hypothyroidism is only partial when judged by behavioural criteria, the medicated individual responding well in simple learning situations but poorly when "higher" capacities, such as the ability to delay a response or to assemble non-contiguous cues are involved. The conclusion must be regarded as tentative, however, for only a small number of rats was used and in any case

since animals starved for the first 24 days and then re-fed were likewise unable to solve the three-table problem, the apparent irreversibility shown by this test would not seem to be peculiarly attributable to hypothyroidism.

(3) Evidence from Enzymological Studies

An enzymological study of the developing brain of the radio-thyroidectomised rat has been recently made by Hamburgh & Flexner (1957) who examined the same region of cerebral cortex as that studied histologically by Eayrs (1956). The activity of four enzymes was investigated: succinic dehydrogenase, cytochrome oxidase, aldolase and acetylcholine esterase. The activity of all increases rapidly in the normal rat from the 10th day after birth. Radio-thyroidectomy was found to be without effect on cytochrome oxidase and aldolase; on the other hand the activity of cholinesterase was depressed between the 5th and 10th days of age and that of succinic dehydrogenase between the 10th and 15th days. Daily therapy with thyroxine or iodothyroglobulin, if started before the 10th day, led to a complete restoration of enzyme activity whereas, if therapy were delayed until the 15th day, activity remained permanently reduced. It is tempting to infer that these observations provide clear cut support for the view that a time factor governs the reversibility of at least some of the maturational defects due to thyroid deficiency. As these workers point out, however, such a conclusion would be premature on the present evidence, further investigation being needed into such factors as the optimum dosage of thyroxine, the dependence on age of the interval between thyroidectomy and the start of therapy and the duration of the treatment with thyroxine.

Are the Effects of Thyroid Deficiency Mediated Directly or Indirectly?

(1) Evidence Favouring a Direct Effect

There can be little doubt that, in amphibia, thyroid hormone is able to exert a direct effect on the development of the nervous system. Kollros (1943) showed that although, during the process of thyroxine-induced metamorphosis in the frog, the maturation of the nervous system was not selectively advanced in relation to that of the body, yet local application of the hormone in the region of the brain-stem facilitated the central linkage of the pathways concerned in the mediation of the lid-closure reflex. The effect proved to be so discrete as to be obtainable unilaterally. Anatomical evidence in favour of a direct influence has been provided by Weiss & Rossetti (1951) who found that, as a result of treating the frog tadpole with thyroxine there was a rapid disappearance of Mauthner's cells (which participate in the mediation of swimming activity) and a local proliferation of smaller neurons believed to be concerned with the integration of limb movements. It seems unlikely that these changes could be secondary to the concomitant disappearance of the tail during late metamorphosis for amputation did not produce the same effect. The findings of Tusques (1956) and of May & Mugard (1955) point the same way in so far as not all regions of the amphibian nervous system seem to respond alike to the action of thyroid hormone but rather are those concerned with the changed habits of the metamorphosed individual primarily affected.

No comparable experiments appear to have been carried out in mammals.

(2) Evidence for an Indirect Effect

(a) *The Influence of Metabolic Processes*

A possible explanation for the maldevelopment of the nervous system in hypothyroidism is that of a general reduction in metabolic processes. While there can be little doubt that a reduced metabolism plays some part in mediating such changes, some additional factor must be postulated, for calorigenic substances such as dinitrophenol, while raising the metabolic rate, will not accelerate the metamorphosis of amphibia nor remedy the symptoms of myxoedema in man. Acetylated thyroxine, which does not raise the metabolic rate, does on the other hand, advance amphibian metamorphosis (Allen, 1938) Such findings underline the dual role of thyroid hormone and suggest that its properties of influencing both the metabolism and the maturation of tissues are exercised to some extent independently.

Reference has already been made to the possibility that thyroid deficiency may, through its effects on the constitution of the inter-cellular matrix, indirectly retard the development of the brain. Gersh & Catchpole (1949) have already pointed out that the processes of growth are associated with a reduction in the viscosity of the ground substance so that the pathologic occurrence of highly polymerised mucoid infiltrations may well be a factor which impedes both the outgrowth of cell processes or the transport of nutrient substances through the extra-cellular medium. Recent work (Goodhead, 1957) suggests that the interstitial substances of the brain

of the rat comprises a muco- or glycoprotein which increases in amount but does not change in its chemical constitution from birth to maturity. Thyroidectomy at birth does not appear to affect the time of appearance or the distribution of this substance although its concentration may be greater than in the normal animal (Horn & Hess, 1958). Too little is known, however, about possible changes in its composition in the cretin to permit further speculation concerning its role as a potential regulator of neural maturation.

(*b*) *The Influence of Vascular Disturbance*

Benda (1947) has claimed that the mental impairment in cretinism is the result of "a metabolic brain pathology produced by the effect of chronic anoxia," believing that changes in the vascular supply to the brain are the main cause. Anoxia is known to impose severe and lasting defects on the developing nervous system both from the point of view of structure (Windle, 1944) and of adaptive behaviour (Becker & Donnel, 1952), and the fact that profound abnormalities do occur in the cardiovascular system in hypothyroidism is well substantiated. Hypercholesterolaemia and a disturbed fat metabolism have been implicated in the degenerative changes which often occur in the capillary endothelium (Leary, 1941) and which may ultimately give rise to the vascular degeneration and sclerosis frequently associated with chronic thyroid deficiency (Kountz, 1951). Stagnant anoxia (Heuper, 1941) resulting from an increased circulation time (McGavack & Schwimmer, 1944), an increased capillary permeability (Lange, 1944) and a reduction in the extent of the capillary bed (Zondek, Michael & Kaatz, 1941) are all factors which could contribute to the impaired cerebral growth of the cretin. More recently Eayrs (1954) has studied, by anatomical methods, the extent of vascular deficiency in the cerebral cortex of chemically thyroidectomised rats. Briefly, the findings showed an increase in the mean size of blood vessels throughout the cortex accompanied by an overall reduction in numbers. The first of these observations is consistent with the view that stagnant anoxia, resulting from chronic venous congestion, is one factor influencing the cerebral development of the cretin. Two additional, but related, factors might also be expected to play a part. First, since a reduced number of capillaries implies an increase in inter-capillary spacing, a larger volume of cortical tissue will be placed at a nutritional disadvantage by reason of its distance from its blood supply; and second, although a capillary enlargement will tend to increase the surface available for metabolic exchange, this increase turns out to be inadequate to offset the reduction attributable to a loss of numbers.

The significance of changes in vascularity is underlined by the results of direct studies of the metabolism of central nervous tissues and hypothyroidism. Thus oxygen consumption by the cerebral cortex of the developing hypothyroid rat, measured *in vitro* by the Warburg technique, does not differ from that of the normal (Fazekas, Graves & Alman, 1951), whereas an increase in the rate of blood flow in cretins medicated for a short period of time is associated with a fall in the arterio-venous difference in oxygen tension rather than in a rise to normal levels (Himwich, Daly, Fazekas & Herrlich, 1942). It may therefore be inferred that the cerebral tissues do not take up oxygen to their capacity and a possible explanation of this phenomenon is to be found in the vascular pattern characteristic of the cretinous rat in which the capillary bed may be inadequate to transport an increased supply of oxygen to the tissues.

These considerations strongly suggest that the cerebral impairment attributable to hypothyroidism may be secondary to vascular disorder. Little, however, is known with certainty about the factors which regulate the density of the capillary bed in the central nervous system. Conclusions based on correlations between regional differences in angio- and cytoarchitecture (Cobb, 1929; Dunning & Wolff, 1937; Campbell, 1939; Scharrer, 1945) give reason to believe that this is determined by the structure and metabolism of the tissue which it serves, and if this be the case, it would be equally valid to postulate that alterations in nervous structure are primarily due to thyroid deficiency, the reduced number of capillaries being adequate to meet the needs of the modified tissues. A third possibility is that, irrespective of any functional inter-relationship between the growth of the vascular bed and that of the neuropil, both are adversely affected by the experimental conditions. It is clearly, in such circumstances, exceedingly difficult to distinguish between cause and effect.

(*c*) *The Influence of Altered Cranio-neural Relationship*

Thyroidectomy during infancy is followed by an increase in the width and height of the brain which is disproportional to the increase in

length (Eayrs & Taylor, 1952). The question therefore arises whether these changes in shape are primarily due to the development of the brain or whether they are secondarily imposed by alterations in the growth of the skull.

There is some evidence to suggest that the latter may well be at least a contributory factor for Dye & Maugham (1929) found that whereas, after thyroidectomy, the growth of the membrane bone forming the calvarium was little affected endochonral ossification at the base of the skull was impaired, giving rise to an endocranial cavity conforming in shape to that of the brain of the cretinous rat. Two other conditions, however, hypophysectomy during infancy (Mortimer, 1937; Walker, Simpson, Asling & Evans, 1950) and chronic deficiency of Vitamin A (Mellanby, 1944; Wolbach 1946, 1947) are both associated with remarkably similar defects suggesting the possibility of some functional connection between the three disorders. At first sight, for instance, it would seem reasonable to attribute the effects of hypophysectomy to hypothyroidism arising secondarily from the withdrawal of thyrotrophic hormone. This seems improbable, however, since these can largely be remedied by giving purified growth hormone (Asling, Walker, Simpson, Li & Evans, 1952). Likewise, the possibility that the similar effects of thyroidectomy and avitaminosis A might be causally linked through the inability to the hypothyroid individual to convert dietary carotene to Vitamin A (Drill, 1943; Cama & Goodwin, 1949) now appears unlikely in the light of finding that the rat's milk, which is the main source of food during the period of development under consideration, is rich in Vitamin A and poor in carotene (Houston, Kon & Henry, 1938). The inter-relationship, if any, between the three deficiencies yielding similar cranio-neural abnormalities thus remains obscure. The fact, however, that both hypophysectomy during infancy and a deficiency of Vitamin A are associated with a disparity between the growth of the brain and cranium so great as to cause herniation of the brain through the foramen magnum suggests that the somewhat less severe effects of thyroidectomy might cause a rise in intra-cranial pressure which could account for the venous congestion, stagnant anoxia and hypolasia of neuropil described earlier. Measurements of the pressure of cerebro-spinal fluid in the cisterna magna (Eayrs, 1956) failed to provide evidence to support this view, but the factors regulating intracranial pressure are extremely complex (see Foley, 1957) and it is possible that the technique used was unsuited to demonstrate a disparity in cranioneurol growth of the type envisaged. The part played by the thyroid in regulating such relationships must remain for the time being an open question.

Conclusions

The foregoing analysis leaves little room for doubt that hypothyroidism, uncomplicated by other factors, is associated with profound changes in central nervous structure which are reflected both in the maturation of innate behaviour and, later in life, in changes in adaptive behaviour consistent with a lowering of sensitivity to sensory input from the external environment. Further than this, however, the available evidence is somewhat less satisfactory. The findings that (i) the pattern of cortical structure in the cretin is not identical with that of a younger animal, (ii) the emergence of automatic behaviour is more retarded and cortical structure more seriously affected in relation to size in hypothyroidism than in very severe inanition, and that (iii) these effects are only slightly if at all ameliorated by giving by growth-promoting substances, all argue for some measure of specificity. At the same time, although it seems at the moment unlikely that a disturbance in cranioneural relationships is a factor underlying these changes, there is presumptive evidence to suggest that some, at least, of the effects of hypothyroidism on cerebral development are mediated indirectly through a combination of such factors as a reduced metabolism, vascular deficiency or alterations in the constitution of the interstitial matrix. It is, however, in relation to the important question of the reversibility of the effects of cretinism and of the variability of the response to medication that the present evidence is in particular need of amplification. Such as is available suggests that both cortical structure and capacity for adaptive behaviour may be adequately restored as a result of therapy, and if the functioning of the cerebral cortex depends primarily upon some statistical relationship between the elements mediating stimulus and response rather than on a precise and topical connectionism, then it is not unreasonable to suppose that a recovery in the density of neuropil would fully restore the animal's behavioural capacity. If, on the other hand, some more precise synaptic relationship between neurons is called for, then it is equally possible that, as a

result of loss of the plasticity present during early stages of development, connections which have failed to mature at the proper time may be unable to do so later and so confer a permanent disability upon the individual. It is true that innately organised responses, though retarded, do eventually appear in the cretinous individual, but the tests of learning so far employed may have been so well within the capacity of the normal rat as to render these inadequate for assessing recovery from the effects of early hypothyroidism. Experiments now in progress and designed to measure and grade capacity for adaptive behaviour using the closed-field apparatus described by Rabinowitz & Rosvold (1951) as a test for "intelligence", and to study associated changes in the electrical activity of the brain seem likely to yield profitable results.

The question of the apparent reversibility of the effects early hypothyroidism in the rat cannot be considered without reference both to the time of onset of thyroid deficiency, and to its duration before the start of medication. Neither of these factors has so far received adequate experimental study. By analogy with the metamorphic effects of thyroid hormone on amphibia it may be that the effect of thyroid deficiency would be less reversible if initiated *in utero* and this possibility needs investigation. Furthermore in most of the studies so far undertaken, athyroidism has not been extended later than the first 24 days of life; and while it is true that, during this period, major developmental changes occur in the central nervous system and the behavioural capacities of the 24-day-old rat seem to differ very little from those of the adult, 24 days, even in so highly-metabolising an animal, would seem to be a short period for the permanent and lasting effects other than those attributable to some direct action of thyroid hormone on interneuronal relationships to become irreversibly established. While, therefore, present knowledge is consistent with the view (expressed by Benda (1947)) that the cerebral dysfunction associated with cretinism is due to metabolic disorder and is reversible provided that such disorder is not of long standing, there is at the moment no experimental evidence regarding the extent to which the changes may become irreversible if left untreated for a greater length of time.

Summary

1. The role of the thyroid gland in the development of nervous tissues cannot be assessed solely by reference to the severe and often lasting defects of congenital hypothyroidism in man. The picture is complicated by inconsistencies in the response of cretinous individuals to medication and by the possible superimposition of other congenital abnormalities upon the endocrine disorder.

2. Ancillary evidence has been derived from experimental studies based largely on the affects of post-natal thyroidectomy in the rat in which the central nervous system is little differentiated at the time of birth.

3. In this species, thyroid deficiency results, as in man, in a retarded appearance of innately organised patterns of behaviour, and later in life in an impaired capacity to react adaptively to environmental change.

4. These deficiencies are associated with changes in the structure of nervous tissues among which a reduced myelination, a hypoplasia of the cell processes forming the cortical neuropil, and an altered pattern of vascularity are prominent.

5. The nervous system of the cretinoid individual differs from that of a younger animal of the same size and from that of a smaller animal of the same age.

6. Thyroid hormone given to the normal individual appears to favour an advanced maturation though not to the same extent as is found in pre-metamorphic amphibia.

7. Substances which, by reason of their influence on protein anabolism might be expected to ameliorate the affects of thyroid deficiency fail to do so.

8. The limited histological and behavioural evidence available suggests that the affects of experimentally induced hypothyroidism in the infant rat are reversible on medication with thyroid hormone. On the other hand, apparently inversible changes have been detected by means of enzymological techniques.

9. There is little evidence for or against the view that in mammalian forms thyroid hormone acts specifically and directly on the development of the conducting elements of nervous tissue as is known to be the case in amphibia. There is good reason to believe, however, that factors such as anoxia, changes in the intercellular matrix and alterations in cranio-neural relationships may secondarily influence the course of neural maturation.

10. These findings help to elucidate the mental retardation of the human cretin in so far as they demonstrate the nature of the severe, and to

some extent specific impairment to cerebral development which may be expected as a result of uncomplicated thyroid deficiency. Any firm inference concerning the reversibility of the effects of this early impairment by medication is at present precluded by lack of knowledge concerning such factors as the significance of the time of onset and duration of thyroid deficiency and by the possible inadequacy of the tests so far used to determine the degree of ensuing disability.

REFERENCES

Allen, B. M. (1938). The endocrine control of amphibian metamorphosis. *Biol. Rev.*, **13**, 1-9.

Asling, C. W., Walker, D. G., Simpson, M. E., Li., G. H., & Evans, H. M. (1952). Deaths in rats submitted to hypophysectomy at an extremely early age and the survival effected by growth hormone. *Anat. Rec.*, **114**, 49-65.

Astwood, E. B. (1954). *Mechanism of action of antithyroid compounds.* In *The Thyroid.* New York: Brookhaven National Laboratory.

Barrnett, R. J. (1949). Thesis: Yale Univ. School of Medicine; quoted in Pincus, G. & Thimann, K. V. *The Hormones.* New York: Academic Press.

Barrnett, R. J. (1950). Experimental production of cretin-like rats. *Yale J. Biol. Med.*, **22**, 313-322.

Becker, R. F. & Donnell, W. (1952). Learning behavior in guinea pigs subjected to asphyxia at birth. *J. comp. physiol. Psychol.*, **45**, 153-162.

Benda, C. E. (1947). *Mongolism and cretinism.* London: Heinemann.

Biel, W. C. (1938). The effect of early inanition upon maze learning in the albino rat. *Comp. psychol. Monogr.*, **15**, 74.

Biel, W. C. (1939). The effects of early inanition on a development schedule for the albino rat. *J. comp. Psychol.*, **28**, 1-15.

von Bonin, G. (1950). *Essay on the cerebral cortex.* Springfield, Ill.: Thomas.

Brewer, D. B. (1951). Myxoedema: An autopsy report with histochemical observations on the nature of the mucoid infiltrations. *J. Path. Bact.*, **53**, 503-512.

Brody, E. B. (1941). The influence of age, hypophysectomy, thyroidextomy and thyroxin injection on simple reaction time in the rat. *J. gen. Physiol.*, **24**, 433-436.

Brody, E. B. (1942). The influence of thyroidectomy and thyroxin injection on the maze behaviour of adult rats. *J. comp. Psychol.*, **34**, 213-221.

Brooks, C. M. (1933). Studies on the cerebral cortex. II. Localised representation of the hopping and placing reactions in the rat. *Amer. J. Physiol.*, **105**, 162-171.

Brown, A. W., Bronstein, I. P. & Kraines, R. (1939). Hypothyroidism and cretinism in childhood. VI. Influence of thyroid therapy on mental growth. *Amer. J. Dis. Child.*, **57**, 517-523.

Bruch, H. & McCune, D. J. (1944). Mental development of congenitally hypothyroid children. Its relationship to physical development and adequacy of treatment. *Amer. J. Dis. Child.*, **67**, 205-224.

Burnham, R. W. (1940). Removal of the thyroid and pituitary glands as related to learning in the rat. *Psychol. Bull.*, **37**, 465.

Burnham, R. W. & Leonard, S. L. (1941). Hypophysectomy and thyroidectomy as related to learning in the rat. I. Preliminary investigation. *J. comp. Psychol.*, **31**, 233-242.

Cama, H. R. & Goodwin, T. W. (1949). Studies in Vitamin A. 9. The role of the thyroid in carotene and vitamin A metabolism. *Biochem. J.*, **45**, 236-241.

Campbell, A. C. P. (1939). Variations in vascularity and oxidase content in different regions of the brain of the cat. *Arch. Neurol. Psychiat.*, (*Chicago*), **41**, 223-242.

Carlson, W. S. (1941). On the relation of thyroid disturbances to performance. *J. comp. Psychol.*, **32**, 475-482.

Cobb, S. (1929). The cerebral circulation. VIII. A quantitative study of the capillaries in the hippocampus. *Arch. Surg.*, (*Chicago*), **41**, 1200-1*h*09.

Conel, J. L. (1947). *The postnatal development of the human cerebral cortex. Vol.* 3. *The cortex of the three-month infant.* Cambridge, Mass.: Harvard University Press.

Drill, V. A. (1943). Inter-relations between thyroid function and vitamin metabolism. *Physiol. Rev.*, **23**, 355-379.

Dunning, H. S. & Wolff, H. C. (1937). The relative vascularity of various parts of the central and peripheral nervous system of the cat and its relation to function. *J. comp. Neurol.*, **67**, 433-450.

Dye, J. A. & Maugham, G. H. (1929). Further studies of the thyroid gland. V. The thyroid gland as a growth promoting and form determining factor in the development of the animal body. *Amer. J. Anat.*, **44**, 331-368.

Eayrs, J. T. (1954). The vascularity of the cerebral cortex in normal and cretinous rats. *J. Anat.*, (*Lond.*), **88**, 164-173.

Eayrs, J. T. (1955). The cerebral cortex of normal and hypothyroid rats. *Acta Anat.*, **25**, 160-183.

Eayrs, J. T. (1956). The effect of Vitamin A on the development of hypothyroid rats. *J. Neuropath. exp. Neurol.*, **15**, 93-102.

Eayrs, J. T. (1959). The effect of protein anabolists on cerebral development in hypothyroidism. *In preparation.*

Eayrs, J. T. & Goodhead, B. (1958). Postnatal development of the cerebral cortex in the rat. *J. Anat.* (*Lond.*), *In press.*

Eayrs, J. T. & Horn, G. (1955). The development of the cerebral cortex in hypothyroid and starved rats. *Anat. Rec.*, 121, 53-62.

Eayrs, J. T. & Lishman, W. A. (1955). The maturation of behaviour in hypothyroidism and starvation. *Brit. J. anim. Behav.*, **3**, 17-24.

Eayrs, J. T. & Taylor, S. H. (1951). The effect of thyroid deficiency induced by methyl thiouracil on the maturation of the central nervous system. *J. Anat.*, (*Lond.*), **85**, 350-358.

Evans, H. M., Simpson, M. E. & Pencharz, R. I. (1939). Relation between the growth promoting effects of the pituitary and the thyroid hormone. *Endocrinology*, **25**, 175-182.

Fazekas, J. F., Graves, F. B. & Alman, R. W. (1951). The influence of the thyroid on cerebral metabolism. *Endocrinology*, **48**, 169-174.

Flexner, L. B. & Flexner, J. B. (1949). Biochemical and physiological differentiation during morphogenesis. IX. The extracellular and intracellular phases of the liver and cerebral cortex of the foetal guinea-pig as estimated from distribution of chloride and radiosodium. *J. cell. comp. Physiol.*, **34**, 115-127.

Flower, C. F. & Evans, H. M. (1925). The repair of dwarfism following the administration of anterior hypophyseal fluid. *Anat. Rec.*, **29**, 383.

Foley, J. (1957). Physiology of increased intracranial pressure. *In Modern trends in neurology* (Ed. Williams). London: Butterworth.

Gersh, I. & Catchpole, H. R. (1949). The organisation of ground substance and basement membrane and its significance in tissue injury. *Amer. J. Anat.*, **85**, 457-507.

Gessell, A., Amatruda, C. S. & Culotta, C. S. (1936). Effect of thyroid therapy on mental and physical growth of cretinous infants. *Amer. J. Dis. Child.*, **52**, 1117-1138.

Goldberg, R. C. & Chaikoff, I. L. (1949). A simplified procedure for thyroidectomy of the newborn rat without concomitant parathyroidectomy. *Endocrinology*, **45**, 64-70.

Goldsmith, E. W., Gordon, A. S. & Charipper, H. A. (1945). An analysis of the effects of continued thiourea treatment in pregnancy on the development of offspring in the rat. *Amer. J. Obstet. Gynac.*, **49**, 197-206.

Goodhead, B. (1957). The development of a ground substance in the cerebral cortex of the rat. *Acta Anat.*, **29**, 297-304.

Goodkind, R. P. & Higgins, H. L. (1941). Hypothyroidism in infants and children: with reference to the ultimate prognosis concerning intelligence and to the withdrawal of thyroid therapy as a diagnostic measure. *New England J. Med.*, **224**, 722-726.

Gordan, G. S., Eisenberg, E., Moon, H. D. & Sakomoto, W. (1951). Methylandrostenediol: a protein-anabolic steroid with little androgenic activity. *J. clin. Endocr.*, **11**, 209-212.

Gudernatsch, J. F. (1912). Feeding experiments on tadpoles. I. Influence of specific organs given as food. A contribution to the knowledge of organs with internal secretion. *Arch. Entwickl.-Mech. Org.*, **35**, 457-483.

Hamburgh, M. (1955). Enzyme activities in the developing nervous system of normal and hypothyroid rats. *Anat. Rec.*, **121**, 304.

Hamburgh, M. & Flexner, L. B. (1957). Biochemical and physiological differentiation during morphogenesis. XXI. Effect of hypothyroidism and hormone therapy on enzyme activities of the developing cerebral cortex of the rat. *J. Neurochem.*, **1**, 279-288.

Hammett, F. S. (1927). Studies of the thyroid apparatus. XXXI. The role of the thyroid and parathyroid glands in the growth of the central nervous system. *J. comp. Neurol.*, **41**, 171-222.

Himwich, H. E., Daly, C., Fazekas, J. F. & Herrlich, H. C. (1942). Effects of thyroid medication on brain metabolism of cretins. *Amer. J. Psychiat.*, **98**, 489-493.

Horn, G. (1955). Thyroid deficiency and inanition. The effects of replacement therapy on the development of the cerebral cortex of young albino rats. *Anat. Rec.*, **121**, 63-79.

Horn, G. & Hess, A. (1958). The effects of hypothyroidism on the development of the ground substance of the cerebral cortex. *J. Anat. (Lond.)*, **92**, 419-424.

Horsten, G. P. M. & Boeles, J. Th. F. (1949). The influence of hypothyroidism on the excitability of peripheral nerves. *Arch. int. Pharmacodyn.*, **78**, 93-99.

Houston, J. Kon, S. K., & Henry, K. M. (1938). On certain vitamins in rat's and in guinea-pig's milk. *Chem. Ind.*, **57**, 276.

Heuper, W. C. (1941). The etiology and causative mechanism of arteriosclerosis and atheromatosis. *Medicine (Baltimore)*, **20**, 397-442.

Hughes, A. M. (1944). Cretinism in rats produced by thiouracil. *Endocrinology*, **34**, 69-76.

Iason, A. H. (1946). *The thyroid gland in medical history*. New York: Froben Press.

Isenschmid, R. (1918). Histologische Veranderungen im Zentral-Nervensystem bei Schildrusenmangel. *Frankfurt. Z. Path.*, **21**, 321-336.

Kollros, J. J. (1943). Experimental studies on the development of the corneal reflex in amphibia. II. Localised maturation of the reflex mechanism effected by thyroxin-agar implants into the midbrain. *Physiol. Zool.*, **16**, 269-279.

Korner, A. & Young, F. G. (1955a). The influence of methylandrostenediol on the body weight and carcass composition of the rat. *J. Endocr.*, **13**, 78-83.

Korner, A. & Young, F. G. (1955b). The effect of methylandrostenediol on the weight and protein content of muscles and organs of the rat. *J. Endocr.*, **13**, 84-89.

Kountz, W. B. (1951). *Thyroid function and its possible role in vascular degeneration*. Springfield, Ill.: Thomas.

Lange, K. (1944). Capillary permeability in myxoedema. *Amer. J. med. Sci.*, **208**, 5-15.

Leary, T. (1941). The genesis of atherosclerosis. *Arch. Path. Lab. Med.*, **32**, 507-555.

Leblond, C. P., Everett, N. B. & Simmons, B. (1958). Sites of protein synthesis as shown by radioautography after administration of S^{35}-labelled methionine. *Amer. J. Anat.*, **101**, 225-271.

Lewis, A. (1937). A study of cretinism in London. *Lancet*, **1**, 1505-1509, **2**, 5-9.

Lishman, W. A. (1953). The effect of radiothyroidectomy on behaviour and on the structure of the nervous system in the albino rat. *Thesis: University of Birmingham.*

Lorente de Nó (1922). La corteza cerebral del ratón. *Trab. Lab., Invest. biol. Univ. Madrid*, **20**, 41-78.

Lotmar, F. (1929). Histopatholgische Befunde in Gehirnen von congenitalem Myxödem (Thyreoplasie). *Z. ges. Neurol. Psychiat.*, **119**, 491-513.

Lotmar, F. (1933). Histopathologische Befunde in Gehirnen von endemischem Kretinismus Thyreoplasie und Kachexia thyreopriva. *Z. ges. Neurol. Psychiat.*, **146**, 1-53.

Mackenzie, G. G. & Mackenzie, J. B. (1943). Effects of sulfonamides and thioureas on the thyroid gland and basal metabolism. *Endocrinology*, **32**, 185-209.

Maier, N. R. F. (1932). The effect of cerebral destruction on reasoning and learning in rats. *J. comp. Neurol.*, **54**, 45-75.

Maier, N. R. F. (1935). The cortical area concerned with co-ordinated walking in the rat. *J. comp. Neurol.*, **61**, 395-405.

Marie, P. Trétiakoff, C. & Stumfer, E. (1920). Etude anatomopathologique des centres nerveux dans un cas de myxoedème congénital avec cretinism. *Encéphale*, **15**, 601-8.

May, B. M. & Mugard, H. (1955). Action de l'ingestion de poudre de thyroïde sur la multiplication cellulaire dans l'encéphale des têtards de *Rana temporaria*. *Ann. Endocr.* (*Paris*), **16**, 46-66.

McGavack, T. H. & Schwimmer, D. (1944). Problems in the treatment of cardiac failure in myxoedema. *J. clin. Endocr.*, **4**, 427-439.

McSwiney, R. R. & Prunty, F. T. G. (1957). Metabolic effects of three testosterone derivatives including 17 α ethyl 19- nor-testosterone. *J. Endocr.*, **16**, 28-40.

Means, J. H. (1948). *The thyroid and its diseases*. Philadelphia: Lippincott.

Mellanby, E. (1944). Nutrition in relation to bone growth and the nervous system. *Proc. roy. Soc.*, **132B**, 28-46.

Meyer, A. E. & Ransom, G. V. (1945). The metabolism of rats after thyroidectomy or during thiouracil treatment and the effect of thyroid feeding. *Endocrinology*, **36**, 259-265.

Millen, J. W., Woollam, D. H. W. & Lamming, G. E. (1953). Hydrocephalus associated with a deficiency of Vitamin A. *Lancet*, **2**, 1234-1236.

Mortimer, H. (1937). Pituitary and associated hormone factors in cranial growth and differentiation in the white rat. *Radiology*, **28**, 5-39.

Mulinos, M. G. & Pomerantz, L. (1942). Some precocious developmental changes produced by adrenal cortical hormones. *Science*, **95**, 484-485.

Parmer, L. G. (1947). Effect of deoxycorticosterone on development of rats treated with thiouracil. *Proc. Soc. exp. Biol.* (*N.Y.*), **66**, 574-575.

Peters, V. B. & Flexner, L. B. (1950). Biochemical and physiological differentiation during morphogenesis. VIII. Quantitative morphologic studies on the developing cerebral cortex of the fetal guinea-pig. *Amer. J. Physiol.*, **86**, 133-157.

Rabinovitz, M. S. & Rosvold, H. E. (1951). A closed-field intelligence test for rats. *Canad. J. Psychol.*, **5**, 122-128.

Radwin, L. S., Michelson, J. P., Kramer, B. & Berman, A. B. (1949). End results in treatment of congenital hypothyroidism: Follow-up study of physical, mental and behavioral developments. *Amer. J. Dis. Child.*, **78**, 821-843.

Ray, R. D., Simpson, M. E., Li., C.H., Asling, C. W. & Evans, H. M. (1950). Effects of the pituitary growth hormone and of thyroxin on growth and differentiation of the skeleton of the rat thyroidectomised at birth. *Amer. J. Anat.*, **80**, 479-576.

Rickey, E. (1925). The thyroid influence on the behavior of the white rat. *Comp. Psychol. Monogr.*, **2**, No. 12.

Rockwell, J. G. (1931). Thyroparathyroid deficiency. *Psychol. Bull.*, **28**, 222-223.

Rolleston, H. (1934). Prognosis in cretinism. *Lancet*, **2**, 372.

Rudolf, G. de M. (1938). The treatment of a cretin with anterior pituitary extract. *Endocrinology*, **23**, 364-366.

Salgado, E. & Selye, H. (1954). The role of the thyroid in the production of cardiovascular and renal changes by methylandrostenediol. *J. Endocr.*, **11**, 331-337,

Salmon, T. N. (1936). Effect of thyroparathyroidectomy in newborn rats. *Proc. Soc. exp. Biol.* (*N.Y.*), **35**, 489-491.

Salmon, T. N. (1938). The effect on the growth rate of thyro-parathyroidectomy in newborn rats and of the subsequent administration of thyroid, parathyroid and anterior hypophysis. *Endocrinology*, **23**, 446-457.

Salmon, T. N. (1941). Effect of pituitary growth substance on the development of rats thyroidectomised at birth. *Endocrinology*, **29**, 291-296.

Scharrer, E. (1945). Capillaries and mitochondria in neuropil. *J. comp. Neurol.*, **83**, 237-243.

Scow, R. O. & Marx, W. (1945). Response to pituitary growth hormone of rats thyroidectomised on the day of birth. *Anat. Rec.*, **91**, 227-236.

Scow, R. O. & Simpson, M. E. (1945). Thyroidectomy in the newborn rat. *Anat. Rec.*, **91**, 209-226.

Scow, R. O. & Simpson, M. E., Asling, C. W., Li., C.H., & Evans, H. M. (1949). Response by the rat thyroparathyroidectomised at birth to growth hormone and to thyroxin given separately or in combination. I. General growth and organ changes. *Anat. Rec.*, **104**, 445-463.

Sholl, D. A. & Uttley, A. M. (1953). Pattern discrimination in the visual cortex. *Nature*, **171**, 387-388.

Simpson, S. L. (1948). *Major endocrine disorders*. London: Oxford University Press.

Smith, P. E. (1933). Increased skeletal affects in A.P. growth hormone injections by administration of thyroid in hypophysectomised, thyro-parathyroidectomised rat. *Proc. Soc. exp. Biol.* (*N.Y.*), **30**, 1252-1254.

Tilney, F. (1933). Behavior in its relation to the development of the brain. Part II. Correlation between the development of the brain and behavior in the albino rat from embryonic states to maturity. *Bull. neurol. Inst.* (*N.Y.*), **3**, 252-358.

Topper, A. (1951). Mental achievement of congenitally hypothyroid children. *Amer. J. Dis. Child.*, **81**, 233-249.

Tredgold, A. F. (1929). *A text-book of mental deficiency*. 5th Ed. London: Baillière, Tindall and Cox.

Tusques, J. (1956). Recherches expérimentales sur le rôle de la thyroïde dans le développement du système nerveux. *Biologie* (*Paris*), **45**, 395-413.

Uttley, A. M. (1955). The probability of neural connexions. *Proc. roy. Soc.*, **144B**, 229-240.

Walker, D. G., Asling, C. W., Simpson, M. E., Li., C.H., & Evans, H. M. (1952). Structural alterations in rats hypophysectomised at 6 days of age and their correction with growth hormone. *Anat. Rec.*, **114**, 19-47.

Walker, D. H., Simpson, M. E., Asling, C. W. & Evans, H. M. (1950). Growth and differentiation in the rat following hypophysectomy at 6 days of age. *Anat. Rec.*, **106**, 539-554.

Warden, C. J., Ross, S. & Zamenhof, S. (1942). The effect of artificial changes in the brain of maze-learning in the white rat. *Science*, **95**, 414-415.

Weil, A. (1941). The chemical constitution of brain, kidneys and heart of white rats in experimental hypothyroidism. *Endocrinology*, **29**, 919-926.

Weiss, P. (1949). Differential growth. In: *The chemistry and physiology of growth* (Ed. Parpart). Princeton: The University Press.

Weiss, P. (1950). An introduction to genetic neurology. In: *Genetic neurology* (Ed. Weiss). Chicago: University Press.

Weiss, P. & Rossetti, F. (1951). Differential growth response of nerve cells to thyroid hormone. *Proc. nat. Acad. Sci., Wash.*, **37**, 540-556.

Wilkins, L. & Fleischmann, W. (1941). The diagnosis of hypothyroidism in childhood. *J. Amer. med. Ass.*, **116**, 2459-2465.

Windle, W. F. (1944). Structural and functional alterations in the brain following neonatal asphyxia. *Psychosom. Med.*, **6**, 155-156.

Wolbach, S. B. (1946). Vitamin A: deficiency and excess in relation to skeletal growth. *Proc. Inst. Med. Chicago*, **16**, 118-145.

Wolbach, S. B. (1947). Vitamin A: deficiency and excess in relation to skeletal growth. *J. Bone Jt. Surg.*, **29**, 171-192.

Woodbury, D. M., Hurley, R. E., Lewis, N. G., McArthur, M. W., Copeland, W. W., Kirschrink, J. F. & Goodman, L. S. (1952). Effect of thyroxine, thyroidectomy and 6-N-propyl-2-thiouracil on brain function. *J. Pharmacol.*, **106**, 331-340.

Zamenhof, S. (1942). Stimulation of cortical-cell proliferation by the growth hormone. III. Experiments on albino rats. *Physiol. Zool.*, **15**, 281-292.

Ziskin, D. E., Salmon, T. N. & Applebaum, E. (1940). The effect of thyroparathyroidectomy at birth and at 7-days on dental and skeletal development of rats. *J. dent. Res.*, **19**, 93-102.

Zondek, H., Michael, M. & Kaatz, A. (1941). The capillaries in myxoedema. *Amer. J. med. Sci.*, **202**, 435-440.

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GROOMING ACTIVITIES AND FREEZING BEHAVIOUR IN RELATION TO EMOTIONALITY IN ALBINO RATS

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Introduction

During an enquiry recently carried out in this laboratory in which an open field situation (Hall, 1934, 1936; Broadhurst, 1957) was used to measure emotionality in albino rats, records were kept of "freezing" behaviour and also of face-washing and fur-scratching, both of which are grooming activities. Since, in some species, e.g. cats and chimpanzees, displacement activity takes the form of grooming (Armstrong, 1950; Tinbergen, 1952) it was considered that findings concerning the relation of freezing behaviour and grooming activity to established measures of emotionality would be of both ethological and psychological interest.

The term "emotionality" as it is most frequently used in comparative psychology, does not refer to individual differences in specific emotions. As Hall showed in a review of animal studies on temperament (1941), terms such as excitability, instability, timidity and fearfulness were grouped under the head of emotionality because investigators so frequently used them to describe similar behaviour in rodents faced with unfamiliar or stressful situations. The traits implied by these terms have not been operationally defined but consideration of the inadequacies of the concept of emotionality is beyond the scope of this discussion: the literature suggests a measure of agreement. Emotionality is a blanket term covering a group of organic and expressive reactions to strange situations. It conveniently describes aspects of the generally excited and upset condition of animals faced with such situations, and it is used in this sense in the ensuing discussion.

Several measures of rodent behaviour in unfamiliar situations have constantly been found to intercorrelate. Activity and emotionality are related, emotional rats being less active and less exploratory than non-emotional. In the open field situation emotional rats are reluctant to leave the wall and approach the centre. They are less likely to eat in unfamiliar situations, and it has been repeatedly found that they show a higher incidence of urination and defecation. Billingslea (1942) carried out a factorial analysis on the intercorrelation matrix obtained from several such measures of emotionality, and on the basis of this, he postulated three factors which he identified as emotionality, timidity and freezing.

Freezing is a response pattern in which the animal adopts a compact crouching posture and remains completely motionless, even nose twitching being absent. Hall (1938, 1941) mentions the occurrence of "freezing or inhibition of movement" in excited and in timid animals, as does Higginson (1930). Curti (1935) and Griffith (1920) found that rats would freeze when confronted with a cat. Since animals without experience of cats would do this, freezing was an unlearned response to this situation. More recently, Levine (1956), having subjected three groups of rats to differentiated "gentling" treatment, which is known to affect aspects of subsequent behaviour, found that the groups differed in activity, urination-defecation frequency and incidence of freezing. All such findings suggest that freezing may be a valid measure of emotionality.

Face-washing and scratching have also been mentioned as indicating emotionality. O'Kelly (1940) kept records of defecation, urination and face-washing and scratching for animals exposed to an illuminated open field for two two-minute trials on five consecutive days. It is significant that whereas urination-defecation frequency diminished with successive trials in the field, face-washing and scratching, which O'Kelly describes as "seemingly non-adjustive reactions" persisted at a fairly constant level throughout. It is evident from O'Kelly's discussion that he regards face-washing and scratching as expressions of emotional disturbance.

But all who work with rats are well aware that they noımally groom a great deal. The suggestion that grooming is a measure of emotionality therefore carries the implication that grooming occurring in test situations is not normal grooming, but of the nature of displacement activity.

The purpose of this discussion is to show that grooming in the open field situation is not

necessarily an index of emotionality or a displacement activity.

Method

Apparatus and Testing Procedure

The open field situation used was a circular enclosure 8 ft. in diameter bounded by an 18 in. high tin-foil wall. The floor was of dark linoleum, marked with five concentric circles and divided into eight segments by four radial lines. The field was illuminated by a 60-watt bulb suspended 4′ above the centre in such a way as to light the centre but leave the circumference relatively dim. The remainder of the room was dark. Testing was conducted between 2 a.m. and 6.30 a.m. when the activity of the animals was at a high level and disturbance was minimal. Each animal was lifted from the home cage and placed at a point half-way between the wall and the centre of the field. Each remained in the field for three minutes. All animals were given one such trial each day for 12 consecutive days.

The following records relevant to the present discussion were kept for each animal:

(*a*) total number of feet traversed in the open field at each trial.
(*b*) urination-defecation frequency.
(*c*) incidence of "freezing" responses.
(*d*) face-washing and scratching.

The Subjects

The experimental group consisted of 15, and the control group of 24, male albino rats. Conditions of rearing had in all respects been held constant. The animals were 60 days old at the inception of testing.

Previous to the experiment steps had been taken to produce differences in emotionality between the two groups. Using a technique closely similar to that of Thompson & Hockman (1956) the six mothers of the experimental animals had been subjected to stressful and presumably anxiety-arousing experiences before and during pregnancy. The control group were the off-spring of six females of the same age and stock which had *not* undergone such experiences. Thompson & Hockman found highly significant differences between experimental and control group offspring at 30-40 days of age, and many of these differences persisted at 130-140 days of age. It was thus anticipated that there would be similar differences in emotionality between the groups used in this enquiry, and such differences were duly established on the basis of behavioural indexes derived from the open field situation. These were:

1. *Activity.* There were significant differences in the mean activity of the two groups over 12 trials.

2. *Urination-defecation frequency* was significantly different at below the 2½ per cent. level of confidence.

The validity of activity and urination-defecation scores in the open field as measures of emotionality in the albino rat was first established by Hall (1934, 1936), and many other investigators have since verified his findings (e.g. Billingslea, 1942; Broadhurst, 1956). The differences between the two groups used in this enquiry were, as far as these two criteria of emotionality are concerned, not only statistically significant but complementary. The group which showed the highest urination-defecation frequency showed the least activity. It was concluded that the experimental group was the more emotional than the control and that a comparison of the freezing and grooming behaviour of the two groups would therefore throw some light on the relationship of these behaviour patterns to emotionality.

Results

Scores were small and irregular and chi-squared tests were used to test for the significance of differences in frequency of rats showing freezing behaviour and frequency of rats showing grooming activity in each group. In the case

Table I. Freezing Behaviour in the Open Field

(Average time in seconds and percentage of animals showing the response in each trial.)

Group		Trials						Total
		1	2	3	4	5	6	
Control	Av. time % subjects	— —	·109 9	·065 4	·087 4	— —	— —	·260 17·5
Experimental	Av. time % subjects	·133 13	·200 13	·466 27	·100 7	·133 13	·166 27	1·2 40·0

Table II. Grooming Behaviour
(Average number of grooming responses and percentage of animals showing the response on each trial.)

Group		Trials						Total
		7	8	9	10	11	12	
Control	Av. no.	·250	·292	·208	·333	·333	·333	2·300
	% subjects	—	—	—	·133	—	·400	·533
Experimental	% subjects	—	—	—	7	—	33	33

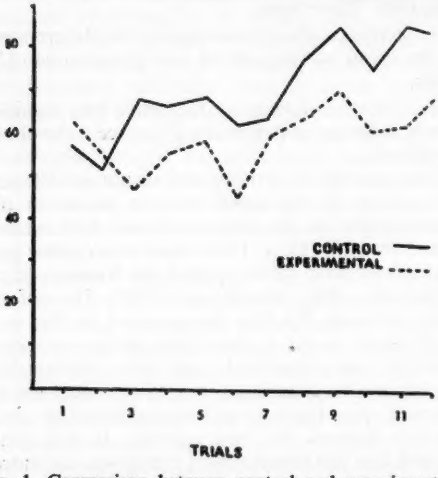

Fig. 1. Comparison between control and experimental groups in mean activity (feet per trial).

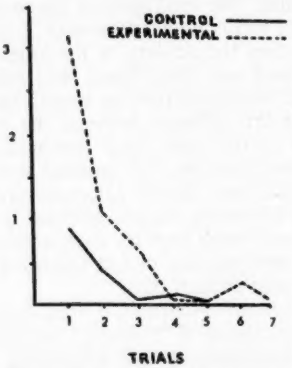

Fig. 2. Comparison between control and experimental groups in mean urination-defecation scores per trial.

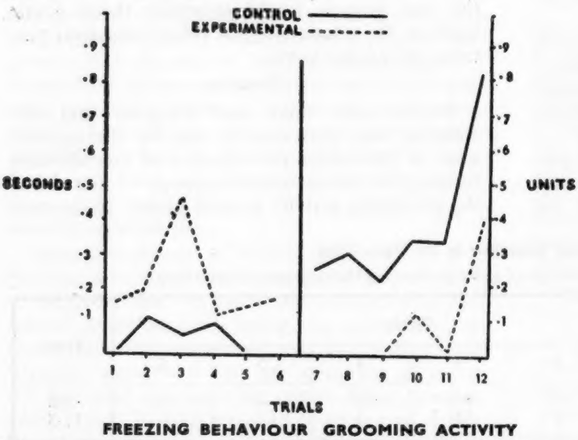

Fig. 3. Comparison between control and experimental groups in mean freezing behaviour in seconds per trial and mean number of grooming responses per trial.

of freezing behaviour the difference was significant at above the 10 per cent. level of confidence and in the case of grooming activity the difference was significant at above the 5 per cent. level of confidence.

Discussion

Consideration of the essential nature of the open field test is necessary to the interpretation of these data. The open field presents to the animal a large, empty, spatially-bounded, illuminated area without corners to offer refuge. The situation is unfamiliar to the cage-reared, experimentally naïve animal, and in view of the habit of the species to cling to walls and avoid light it may be assumed to be to some degree or other a fear or anxiety-provoking situation. It

presumably activates a drive to escape which is then blocked by external circumstances or one which comes into conflict with exploratory tendencies. It may safely be assumed that the situation is initially disturbing to the animal. But since the animal is repeatedly exposed to the situation, it must lose its strangeness and become progressively less disturbing. For this reason truly emotional responses should decrease with successive trials, and non-emotional behaviour, normal everyday activities, should increase. Hall (1938) found "a sizeable relationship" between the adjustment of individual animals to the field as measured by excretory behaviour and their adjustment as measured by their willingness to eat in the test situation.

On this criterion the results of this enquiry support the hypothesis that freezing is a useful index of emotionality. In both groups, freezing was confined to the first six trials. Moreover, during these trials, all instances of recorded urination and defecation occurred, and activity was at its lowest. After the sixth trial, as the situation became familiar, freezing as well as urination and defecation ceased while activity increased. This provides evidence that the open field situation, even without the addition of noise (Broadhurst, *op. cit.*) and with low illumination, was disturbing to both groups at the outset.

Although the difference between the two groups was not statistically significant, it was in the expected direction; the more emotional experimental group showed more freezing behaviour and showed it for longer. These findings support those of Hall, Higginson and Levine.

Grooming activities present a different picture. They are recorded for the first time on the seventh trial for the control group and on the ninth trial for the experimental group. Not only do the control animals show grooming activity earlier but they groom more frequently. Further, grooming behaviour commences after freezing, urination and defecation have ceased. Fig. 3 shows that not only is there no overlap between the occurrence of freezing and grooming over the 12 trials but there is no overlap between the scores of the experimental and control groups for freezing and grooming.

It is deduced that the grooming behaviour shown in the test situation used was not correlated with emotionality and could not be regarded as displacement activity. Armstrong and Tinbergen (*op. cit.*) agree that one of the conditions for the appearance of displacement activity is a conflictful and frustrating situation such that "excess of drive" will be involved. The open field is ostensibly such a situation since, as noted, some degree of antagonistic motivation must be present in at least the initial presentations. This will, however, decrease with successive trials. Thus, behaviour of the nature of displacement activity would be expected to appear in the earlier trials and decrease in the later. It would also be expected to appear more frequently in emotional animals with low frustration-tolerance. Neither of these expectations are borne out by this study of grooming.

Tinbergen stresses the irrelevant nature of displacement activity and its appearance "out of context." Psychologists (*cf.* O'Kelly, *op. cit.*) analogously stress the non-adjustive aspects of emotional behaviour. In fact, there is nothing necessarily irrelevant or non-adjustive about the behaviour of rats which groom in the open field any more than there is about the behaviour of rats which eat in the open field. Indeed, if eating indicates adjustment, grooming, far from being a symptom of non-adjustment, may also do so.

It is not implied that grooming may not indicate emotionality under other conditions. (The situation in which it was observed in this study was not a markedly stressful one as compared with that of Broadhurst (1957)). In a previous enquiry (Yule, 1957) in which the first reactions of a group of 23 rats to an unfamiliar cage were under observation, grooming constantly appeared along with active exploration. On both these occasions there had been severe extraneous disturbances. It is interesting that the grooming activity which then occurred was described as "intense."

Displacement grooming almost certainly exists in rats and requires objective description. The findings of this study suggest that even in situations designed to induce conflict and thwarting, grooming cannot lightly be assumed to be displacement activity or to indicate emotionality. Freezing, on the contrary is a useful index of emotional disturbance.

Summary

Two groups of experimentally naïve male rats were used. The experimental group (N=15) were the offspring of six females which had been subjected to anxiety-arousing experiences before and during pregnancy. The control group (N=24) were the offspring of females of the same age and stock which had not undergone this treatment. Rearing conditions of both groups were held

constant. Differences in emotionality between the experimental and control groups were established by well-validated measures taken in an open field situation. Records of freezing behaviour and grooming activity kept throughout the test series were analysed. It was concluded that freezing behaviour is a valid measure of emotionality and cannot be interpreted as displacement activity without careful consideration of the conditions under which it is observed and its relation to other measurable aspects of behaviour.

REFERENCES

Armstrong, E. A. (1950). *Society for Experimental Biology*. Cambridge University Press.

Billingslea, F. Y. (1942). Intercorrelational analysis of certain behaviour salients in the rat. *J. comp. Psychol.*, **36**, 203-211.

Broadhurst, P. L. (1957). Determinants of emotionality in the rat. I. *Brit. J. Psychol.*, **48**, 1-12.

Curti, M. W. (1935). Native fear responses of white rats in the presence of cats. *Psychol. Monogr.*, **46**, 78-98.

Griffith, C. R. (1920). The behaviour of white rats in the presence of cats. *Psychobiol.*, **2**, 19-28.

Hall, C. S. (1934). Emotional behaviour in the rat. I. Defecation and urination as measures of individual differences in emotionality. *J. comp. Psychol.*, **18**, 385-403.

Hall, C. S. (1936). Emotionality in the rat. III. The relationship between emotionality and ambulatory activity. *J. comp. Psychol.*, **22**, 345-352.

Hall, C. S. (1938). The inheritance of emotionality. *Sigma Xi Quart.*, **26**, 17-27.

Hall, C. S. (1941). Temperament: A survey of animal studies. *Psychol. Bull.*, **38**, 909-943.

Higginson, G. D. (1930). The after-effects of certain emotional situations upon maze learning among white rats. *J. comp. Psychol.*, **10**, 1-10.

Levine, S. (1956). A further study of infantile handling and adult avoidance training. *J. Personality*, **25**, 70.

O'Kelly, L. I. (1940). The validity of defecation as a measure of emotionality in the rat. *J. genet. Psychol.*, **23**, 75-87.

Tinbergen, N. (1952). Derived activities. *Quart. Rev. Biol.*, **27**, 1-32.

Thompson, W. R. & Hockman, C. H. (1956). The influence of pre-natal maternal anxiety on emotionality in young rats. *Amer. Psychol.*, **11**. ?

Yule, E. P. (1957). The Open Field test. *Proc. S.A psychol. Assoc.*, 1957-1958.

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THE EFFECT OF RESTRAINT UPON COPULATORY BEHAVIOUR IN THE RAT

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Ejaculation in the rat is preceded by a series of intromissions each separated from its predecessor by a short intercopulatory interval (ICI). When these intervals are artificially prolonged the number of intromissions required before ejaculation is effectively decreased (Gerall, 1958; Larsson, 1956; Rasmussen—unpublished), an extension to 1 minute duration reducing the frequency of intromission by half its normal value. Enforced intervals of up to 5 minutes give similar results, but short restraints lasting 15 seconds are ineffective. These findings show that the time factor plays an important part in regulating the processes of excitation which underly this aspect of mating behaviour, but so far the precise relationship between the duration of the ICI and number of intromissions necessary to achieve ejaculation has not been determined. The present experiment describes the effect of varying this interval from 0·1 minute to 2 minutes.

Materials and Methods

Animals

Observations were made on the mating behaviour of eleven male rats approximately 12 months old whose mean weight was 372g. (range 346-404g.). All had previously taken part in similar experiments. The females used for mating were treated with 10μg. oestradiol benzoate 36 hours before being presented to the male.

Conduct of Tests

The animals were observed in open cages placed on the laboratory floor. After the male had been given time to adapt to the mating cage a female was introduced and was gently withdrawn as soon as intromission had occurred. The female was then reintroduced after a specified interval of time and again withdrawn immediately after the second intromission. This procedure was repeated until ejaculation had taken place, after which the male was rested for 4-5 days before further testing.

Measurement of Intercopulatory Intervals

A stopwatch graduated in 1/100 sec. was used to time (1) the interval between the presentation of the female to the male and the entry of the penis into the vagina (copulatory latency), and (2) the enforced intercopulatory interval, measured from the moment of intromission to the next presentation of the female. Intercopulatory intervals of 0·0 (*ad lib.*), 0·1, 0·2, 0·4, 0·6, 0·8, 1·0 and 2·0 minutes were enforced in this way, the performance of each rat being observed in relation to each ICI in accordance with a prearranged schedule.

Results

Normal Duration of the Intercopulatory Interval

The duration of the ICI in the unrestrained rat is illustrated in Fig. 1, which shows that 19 per cent. of all intervals were shorter than 0·1 minutes, 61 per cent. shorter than 0·2 minutes, and 85 per cent. shorter than 0·4 minutes. Only one interval was longer than 0·6 minutes.

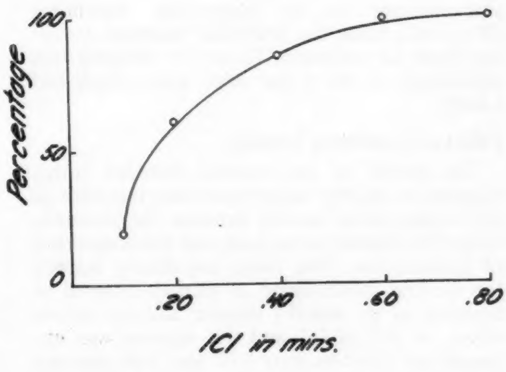

Fig. 1. The cumulative distribution curve showing length of the ICI in animals copulating *ad lib*. The abscissa gives the length of the ICI in hundredths of a minute, the ordinate the percentage of intervals not exceeding each duration.

Effect of Enforced ICI on Frequency of Intromission

The relationship between the number of intromissions preceding ejaculation and the duration of an enforced ICI is given in Fig. 2. When the animals were allowed to copulate *ad lib.*, the mean number of intromissions was 7·8. Prolongation of the ICI from 0·2 to 0·4 minutes resulted in a decrease in the number of intromissions from 8·9 to 5·2, a still greater reduction being recorded when the intervals were extended

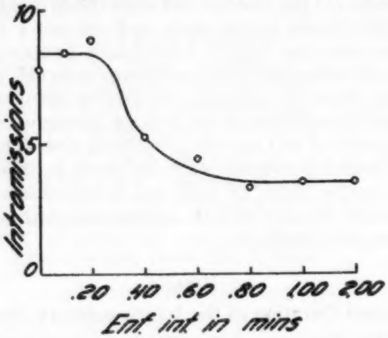

Fig. 2. The effect of restraint on the number of intromissions preceding ejaculation. The abscissa gives the length of the enforced ICI, and the ordinate the mean number of intromissions preceding ejaculation.

to 0·6 and 0·8 minutes. Thereafter, no further decrease took place even when the interval was prolonged to 2 minutes. Analysis of variance showed the overall decrease in the number of intromissions to be statistically significant ($P > 0{\cdot}001$) while the individual decrease resulting from an enforced ICI of 0·4 minutes was significant at the 5 per cent. level (single-tail t-test).

Effect of Copulatory Latency

The length of the interval between intromissions is slightly longer than that recorded as ICI owing to the latency between the presentation of the female to the male and the occurrence of intromission. The mean copulatory latency for the first intromission of animals allowed to copulate *ad lib.* was 0·1 minute, and for rats in which an ICI of 0·1 and 0·2 minutes was enforced the latencies were 0·07 and 0·06 minutes respectively. When the ICI exceeded 0·2 minutes the male became highly excited, hurrying to the female and copulating with the shortest possible latency. Premature ejaculation was sometimes seen. On two occasions when the female was dropped into the mating cage the male took a few steps forward, stopped suddenly and ejaculated in the air 20-30 cm. away from the female.

Discussion

These results emphasise the importance of the variable of time for the elicitation of mating behaviour. Successive intromissions may be considered as building up an excitatory state which culminates in the ejaculatory reflex. Each intromission makes its individual contribution to this rising excitation, the extent of which, however, depends on the time relationships of the sequential sensory inputs. When a very short interval separates two copulations the excitatory effect of the first intromission has not reached its maximal height before that of the second supervenes. The full effect of each intromission does not appear to be realised for about 0·5 minutes and since, in the unrestrained rat, the intromissions succeed each other at very short intervals, the maximal effects of each are never attained. When, however, intercopulatory intervals are artificially prolonged and the full effect of each intromission can be utilised and the number of copulations necessary to cause ejaculation radically lowered, even to the extent that the reflex can appear in the absence of sensory stimulation from the glans penis. The optimum duration of the enforced ICI would seem to lie between 0·6 and 0·8 minutes, and the failure of longer intervals to cause any further decrease in the number of intromissions suggests that after 1·0 second the excitatory effect of each intromission begins to wane.

Summary

Intervals, ranging from 0·1 to 2·0 minutes, have been enforced between the several intromissions of penis into vagina which comprise the copulatory behaviour of the rat.

The number of intromissions required for ejaculation is reduced as a result of increasing this intercopulatory interval. This reduction becomes significant when an interval of 0·4 minutes is enforced and is even more marked after an interval of 0·6 minutes.

In such circumstances the animals become excited, show a reduced copulatory latency, and may exhibit premature ejaculation.

Acknowledgments

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REFERENCES

Gerqll, A. A. (1958). Effect of interruption of copulation on male guinea pig sexual behaviour. *Psychol. Rep.*, **4**, 215-221.

Larsson, K. (1956). *Conditioning and sexual behaviour in the male albino rat*. Stockholm: Almqvist & Wiksell. p. 269.

Rasmussen, E. W. The effect of an enforced pause between each coitus on the number of copulatory necessary to achieve ejaculation in the albino rat. *Unpublished manuscript*.

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SOCIALISATION AND IMPRINTING IN BROWN LEGHORN CHICKS

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Introduction

Detailed investigations of wild Mallard ducklings (Ramsay & Hess, 1957), and of New Hampshire Red chicks (Jaynes, 1956, 1957), have shown the critical period during which imprinting is possible in these two species to have upper limits of 20 and 54 hours, respectively. Following William James' early lead, several workers have suggested that the restriction of imprinting to a critical period is due to the development of fear or avoidance of moving objects, so that following is inhibited and imprinting therefore no longer possible (Verplanck, 1955; Hinde, Thorpe & Vince, 1956). This hypothesis has received support from Hess (1957) who has shown that the success of imprinting in Mallard ducklings depends on the amount of following; that the end of the critical period coincides with the appearance of "emotionality"; and that certain drugs which reduce emotionality (chlorpromazine, meprobamate), also extend the critical period.

Fear is probably not the only factor involved in terminating the critical period since some Mallard ducklings (Weidmann, 1956), and some domestic chicks (Jaynes, 1956; Guiton, 1958) which have exceeded the age limit show neither fright nor following-responses to a strange moving object. Moreover, studies with Brown Leghorn chicks (Guiton, 1958) have shown that the following-response to a strange object is lost at an earlier age in socially-reared chicks than it is in isolated ones; and that absence of a following-response in socially-reared birds is not invariably associated with any sign of fear or avoidance of the object. It was also found that chicks, reared together to an age when they no longer followed an unfamiliar object, and subsequently isolated for some days would then follow that object, whereas the non-isolated controls did not respond.

This reappearance of the following-response after isolation may seem, at first sight, to indicate that no irreversible process is involved in the original loss of the response. It can be supposed that the tendency to follow an unfamiliar moving object decreases when a chick receives certain visual, tactile or other types of stimulation from other chicks, but increases again after this stimulation has ceased for a certain length of time. According to this *drive-satiation hypothesis* the following-response to a strange object would persist for an indefinite period in chicks isolated from all social contact until the age of exposure and would be independent of any learning.

The results can be equally well explained, on the other hand, by supposing that the chicks learn to follow one another during the initial period of social-rearing; and that this response is subsequently generalised to other stimulus-objects—any moving object—but only after a prolonged period of isolation from other chicks. Without this period of isolation before exposure to the moving object, no following-response is obtained because the chick can still discriminate the moving object from its fellow chicks. It therefore ignores the object while searching for its companions. On this *generalisation hypothesis*, the response to an unfamiliar object could still occur in chicks isolated after social contact, even at an age when it may have become difficult or impossible to evoke in totally isolated, socially-inexperienced chicks, due to the development of fear.

The following experiments were carried out to test these hypotheses.

Methods and Materials

The chicks were F_1 hybrids of two inbred lines of the Brown Leghorn flock at the Poultry Research Centre. At 4 to 24 hours old each chick was transferred from its individual hatching box in the incubator, to an individual cage in a constant temperature room and supplied with food and water. While in these cages, the birds had no visual or physical contact with any moving objects or with one another, so that social experience (other than that of an auditory kind) prior to experimental treatments, was confined to the very brief period of handling when they were transferred. The room temperature was gradually reduced from 37°C on the 1st day to 35·5°C on the 4th day.

Two models were used for imprinting the birds or for testing their following responses: Model M, a light green box 40 cm. long × 17

cm. high, × 7 cm. wide, and having a head, tail and four legs; and Model B, a brick red box 25 cm. × 28 cm. × 12 cm., with a tail, head and two legs. The head, tail and legs were dissimilar in the two models and were incorporated to make the models more easily distinguishable by the chicks.

These models could be suspended from the ends of an overhead arm rotated by an electric motor. By means of this apparatus they were propelled at a constant speed of 14 cm. per second along a circular route 180 cm. in diameter. Each model contained a loudspeaker connected by wiping-contacts to a tape recorder. This was adjusted to play a continuous-loop recording of a broody hen calling her chicks (clucking).

The response measurements made were: (1) the number of seconds per 5-minute period, during which the chick walked within 30 cm. to the side of, or behind the model, or not more than 15 cm. in front of it, and in the same direction; and (2) the time taken for the chick to make its first full response, by which is meant the bird making a direct approach to the model or walking with it, while making at the same time, contentment calls.

Training sessions. These took place when the birds were from 20 to 54 hours old. Each one was transferred in a small enclosed wooden box from the cage to the runway, and there placed 60 cm. in front of the stationary model and about 20 cm. to the side of its track. The model was then started up, and driven along its circular route without interruption for 30 minutes: clucking for the first 25 minutes, silent for the last 5 minutes. The amount of following was measured during the last two 5-minute periods.

Test sessions. These also lasted 30 minutes, but differed from the training sessions in that the model was silent throughout, and following was measured during the 2nd, 4th and 6th 5-minute periods. Test sessions took place about 72 hours after training sessions, when the birds were between 96 and 126 hours old.

All chicks were trained or tested individually. The temperature of the runway was maintained at 25-27°C.

Experiments

Experiment 1. Generalisation of the Following-response

The aims of this experiment were: (1) to compare the effect of an unfamiliar moving object on birds totally isolated from the day of hatching, with its effect on birds which were only isolated after some social contact, in order to find out whether the reappearance of the following-response after isolation is due to earlier social experience; (2) to determine if chicks imprinted on one model generalise their response to other models, when isolated; and (3) to see whether the inhibitory effect of socialisation on the following-response can be distinguished from the effect of fear.

Thirty four chicks were divided into five groups each of which received one of the following treatments:

1. *Socialisation-isolation.* Seven chicks were transferred from their cages to a social brooder at 20 to 54 hours of age, left there for three and a half hours, and then placed, still as a group, in the experimental runway for 30 minutes without a model. Each bird was then returned to its isolation cage. Approximately 72 hours later, each chick's following-response was tested with Model B.

2. *Imprinting-isolation.* Six chicks were imprinted—trained to follow Model M—at the age of 20 to 54 hours, replaced in their isolation cages, and then tested with Model B 72 hours later.

3. *Total isolation.* Nine chicks received no training or social experience until, at the age of 96 to 126 hours, they were tested with Model B Six of these chicks were, however, placed singly in the runway for 30 minutes each at the age of 20 to 54 hours—but without a model—to habituate them to the experimental situation.

4. *Imprinting-socialisation.* Six chicks were trained to follow Model M, as in group 2, but were then reared for the next 72 hours in a social brooder, before being tested with Model B.

5. *Total socialisation.* Six chicks were reared together in a socail brooder from the age of 20 to 54 hours until they were tested with Model B at 96 to 126 hours old.

The whole experiment was spread over three consecutive weeks and involved three separate broods.

Results. The results of test sessions are summarised in Table I. The differences between the scores of the following groups are statistically significant:

Groups	t	Number of degrees of freedom	P<
1 and 2	2·52	11	0·05
1 and 3	2·68	14	0·02
3 and 5	2·47	13	0·05
1 and 4	3·49	11	0·01

Table I. Mean Total Duration of Following in each Group of Model B during Test Sessions

Group and Treatment	Mean total duration of following, in seconds	Number of birds in group	Standard error of the mean
1. Socialisation—isolation	136	7	32·14
2. Imprinting—isolation	325	6	74·35
3. Total isolation	41	9	11·64
4. Imprinting—socialisation	16	6	12·36
5. Total socialisation	10	6	4·76

It follows from these data that the differences between the scores of Groups 2 and 3, 2 and 4, 1 and 5, and 2 and 5 are also statistically significant. There is, however, no significant difference between the scores of Groups 3 and 4, or between those of 4 and 5.

These differences were due in part to differences in the number of birds responding to the model; differences in the amount of following in the responding birds; and lastly, in the time taken for the birds to start following. (Table II).

There was no apparent difference in behaviour between the three birds of Group 3 which had received no habituation experience before the test, and the six that had: their respective mean scores were 44 seconds (three birds) and 39 seconds. Moreover, of the two groups in which there was virtually no following, one (Group 4) consisted of birds with prior experience of the runway, while the other (Group 5) consisted of inexperienced birds. Limited experience of the experimental situation at an earlier age can therefore have had little effect on the results compared with the effect of social experience and imprinting.

Since chicks of Groups 1 and 2—previously exposed to other chicks or to Model M—responded to Model B much better than chicks with no such treatment (Group 3), it is evident that the following-response was facilitated by

Table II

Group and treatment	Mean score of responding birds: duration of following in the 2nd, 4th and 5th 6-min. period (seconds)			
	5-10 mins.	15-20 mins.	25-30 mins.	
1. Socialisation—isolation	30	33	72	
2. Imprinting—isolation	88	126	111	
3. Total isolation	5	27	33	
4. Imprinting—socialisation	0	9	45	
5. Total socialisation	0	28*	2*	
	Number of birds per group which had made a full response by the 2nd, 4th and 6th period			Number of birds in group
1. Socialisation—isolation	6	7	7	7
2. Imprinting—isolation	6	6	6	6
3. Total isolation	1	5	7	9
4. Imprinting—socialisation	0	1	2	6
5. Total socialisation	0	0	0	6

*Following, but no full response.

the previous experience. This effect, however, was only evinced in those chicks where the social contact was restricted to the second day of life, for Groups 4 and 5—in both of which the chicks remained together until they were tested—had lower following scores than the totally isolated birds (Group 3).

Emotional Behaviour

Four modes of behaviour are included in this category: avoidance of the model; crouching; trying to escape from the runway; and distress calls. As a rule, when avoidance of the model was strong the bird was rather silent; when crouching it was always silent except for a few seconds before standing up, when it started to give distress calls. Loud and persistent distress calls chiefly occurred as the chick walked about the runway, apparently searching for something; or they occurred in chicks trying to get out of the runway, though such birds were occasionally silent.

Avoidance of the moving model was most marked in the totally isolated birds (Group 3), (Table III). In spite of this, seven out of the nine chicks in this group eventually followed, whereas, of the totally socialised chicks (Group 5) none gave a full following-response although showing less fear of the model. The essential difference between these two groups was this: in Group 3 there was avoidance of the model at the start of the test, but at some moment before the end of it, fear rapidly fell and the bird suddenly switched over to following; in Group 5, however, where avoidance (or crouching) ceased completely in five out of six chicks, this was succeeded not by following but by "searching" with distress calls, the model being almost altogether ignored. Group 4 chicks (imprinting-socialisation) displayed much the same pattern of behaviour as Group 5, though here, two out of the five chicks which had ceased to avoid the model before the end of the test, then started to follow it.

Table III. Incidence of Strong Avoidance Behaviour during Test Sessions

Group	Number of chicks showing strong avoidance	Number of chicks in group
1. Socialisation–isolation	2	7
2. Imprinting–isolation	1	6
3. Total isolation	6	9
4. Imprinting–socialisation	2	6
5. Total socialisation	1	6

Although the chicks of Groups 1 (socialisation -isolation) and 2 (imprinting-isolation), like those of the three other groups, either courched or avoided the model at the beginning of the test, three of them very strongly, all but one of them had switched to following before the end of 10 minutes, and thereafter showed few or no signs of being emotional; and the last one had switched by the 15th minute.

Conclusions

A comparison of the behaviour of the totally isolated chicks with that of the chicks reared socially until the test, confirms that, as previously indicated (Guiton, 1958), socialisation leads to an earlier loss of the following-response. This effect does not appear to be the consequence of increased fear of the model in socialised chicks, although non-following in the isolated birds may have been primarily due to fear of the model.

However, since better following was obtained in the socialisation-isolation group than in either of the above groups, it would seem that previous social experience is necessary if the response is to persist, and that subsequent isolation causes the response to be generalised to strange objects. A comparison of the test performance of Group 2 chicks (imprinting-isolation) and Group 4 chicks (imprinting-socialisation) supports this interpretation, since the response established during training is only generalised to a strange model if the first experience is not interfered with by subsequent socialisation. The superiority of Model M-trained chicks over socialised-isolated ones (Group 1) with respect to the response to Model B, may well be due to the much greater similarity of Model M to Model B than of a chick to Model B; or to the circumstance that social contact involved much more actual following in the one case—chicks trained with model M—than in the other.

If these interpretations are correct then it is probable that continuously socialised chicks become sufficiently imprinted or conditioned to one another to be able to discriminate between a

Table IV. The Mean Time (in seconds) Taken to Respond to Each Model

Group	Model M	Model B	Difference
M-trained chicks	154	259	105
B-trained chicks	223	143	80

chick and a strange moving object such as a box, and that in the test situation it is the absence of its companions rather than fear of the strange moving object that inhibits the socialised chick from following that object.

Experiment 2. Discrimination between Models

The response of M-trained chicks to Model B in Experiment 1, could conceivably mean that the birds were inherently incapable of discriminating between the two models and not, as suggested, that the response was generalised because the birds were isolated after their training with Model M. An experiment was therefore carried out to test the chick's ability to discriminate between the two models presented simultaneously after a previous training session with one of the models only.

The chicks were divided into two groups, the birds of one receiving training with Model M (Group M), and those of the other with Model B (Group B), both at the age of 20 to 54 hours. The training sessions and the method of scoring were the same as those in Experiment 1. In the test sessions, carried out 72 hours later, the chicks were transferred from their isolation cages to the runway where they were placed centrally, midway between Models M and B which were situated diametrically opposite to one another. As soon as the chick was in place and released from its box, the two models were set in motion in the same direction round the runway. The time taken by each chick to start following each model, and the number of seconds which it spent following each model during the 2nd, 4th and 6th five-minute period, were both scored.

A preliminary experiment indicated that the effect of the previous training was partly counteracted by an inherent preference for Model M. Physical contact between chick and model appears to have a strong stimulating effect on following, and inequalities in this respect were thought to account for the above difference. In the definitive experiment, therefore, the legs of the models were removed, and the models themselves were sufficiently raised off the ground to give the chick complete head-clearance.

Results. The first following-response was correct—that is, to the training model—in eleven out of the twelve chicks. The exception was a B-trained chick (Table V). In spite of this high initial degree of discrimination, all but one chick —an M-trained bird—subsequently responded to the other model as well (Table IV).

The relative amounts (group means) by which Model M was followed during the test by Group M and Group B chicks, is given in Table V. The statistically significant difference between the scores of the two groups ($t=2{\cdot}6$, arc sin transformation; $P<0{\cdot}05$ for 10 degrees of freedom) shows that the nature of the training continued to exert an influence. The fact that the mean score of Group B chicks was not significantly different from 50 per cent., and only one out of the six birds in this group showed a pronounced preference for Model B, suggests however, that an inherent preference for Model M still existed after physical contact between the chicks and the models had been eliminated.

This preference might be explained by supposing that Model B was a less stimulating object than Model M. However, although the mean

Table V. Number of Chicks in each Group making a Correct First Choice between Models M and B; and the Mean Relative Amount by which Model M was followed, in each Group.

Group	Number of birds making correct 1st choice	Number of birds in group	Mean following score for Model M, as percentage of total following score for both models.
M-trained	6	6	88
B-trained	5	6	50

training score for Group M was greater than that of the other group, the difference was not significant at the 5 per cent. level of confidence ($t=2\cdot12$, for 10 degrees of freedom).

Whereas the mean following score of M-trained birds tested with Model B alone (Experiment 1, Group 2) was 325 seconds, the similarly trained chicks in this experiment followed the same model for an average of only 38 seconds out of a total average amount of following of 261 seconds for both models. In Experiment 1 the high level of response to the strange model was, therefore, quite clearly due to the absence of the model used for imprinting.

Experiment 3. Group Behaviour in Socialised Chicks

The effect of socialisation on chicks is similar in many respects to that of imprinting (Experiment 1). If it is assumed that with continuous socialisation chicks become sufficiently imprinted or conditioned to one another to be able to discriminate between a fellow chick and a strange box, then their emotional behaviour in the test situation: "searching" and giving distress calls (Experiment 1, Group 5), can be supposed to be the immediate consequence of their isolation from other chicks. That this is so, is well shown by the following observations.

1. Six chicks, socialised from the age of 20 to 54 hours onwards, were placed at the age of 96 to 126 hours around the perimeter of the runway about 50 cm. apart, and observed for 30 minutes. For the first 6 minutes all chicks crouched silently. In the 7th minute one chick started to give distress calls, softly and hesitantly at first, then boldly and loudly as it began to walk about; by the end of the 8th minute the other five chicks had, one by one, followed suit. Soon after this the chicks began to join up: the first two coming together after 7 minutes 45 seconds, and a third one joining them a few seconds later. Distress calls ceased to be given by a chick within 5 seconds of joining up. By the beginning of the 13th minute all six chicks had come together, and the distress calls had entirely ceased and been replaced by contentment calls.

From the 13th to the 25th minutes there were no more distress calls. During this time the chicks remained close together, scratching and pecking at the ground, and giving a continuous "twittering" of contentment calls. No chick ever ventured more than about 20 cm. away from its companions.

After 25 minutes they were forcibly scattered by waving a piece of hardboard overhead, and this at once produced a great volume of distress-calls which, however, died down again as they joined up, within about 30 seconds of being scattered.

2. (*a*) Six other chicks of the same age were transferred from their social brooder to the runway, in a group. They immediately all crouched silently, but at the end of 40 seconds one chick got up and gave distress-calls until the 70th second. After 1 minute 35 seconds all six chicks had risen and begun pecking on the floor and giving contentment calls. Occasionally distress calls were heard after this for 2 minutes, but by the end of the 5th minute these had entirely ceased. The contentment calls, pecking and scratching continued with little interruption, the group of chicks moving very little and very slowly around the runway.

(*b*) After 20 minutes six other (ringed) chicks were placed, one at a time, and in turn, in the runway about 140 cm. away from this group of chicks. The behaviour of each ringed chick was observed for 5 minutes. It was then removed and the next chick put in its place, and so on.

Each ringed chick behaved in the following manner: first, it crouched silently for some seconds; then it started giving distress-calls which increased in volume as it stood up and began to walk. Then, after a further interval of seconds the bird switched over to giving contentment calls and ran towards the group of six chicks; hesitated when about 30 cm. away from it, giving more distress calls, and finally joined the group. With but one exception, the distress-calls then ceased. The one exception continued its calls, but intermittently, to the end of the 5 minutes. The times taken by each chick to complete each stage are given in Table VI.

(*c*) After the sixth ringed chick had been tested and removed, the original six making up the group were left in the runway, and the two models M and B, legless as in Experiment 2, were started up on their circular run. With these models continuously moving for the next 45 minutes, observations were made on the behaviour of the chicks during the first and last 15 minutes of the period.

As far as could be observed all the chicks behaved alike at any one moment. The group was on the periphery of the runway within about 15 cm. from the track of the models for the whole period. During the first 3 minutes the passage of one or the other model gave rise to an increase of movement and excited "twittering" as each chick

Table VI.

Chick	Time taken to start distress calls	Time taken to start moving towards other chicks	Time taken to join up with group
1	10 seconds	30 seconds	75 seconds
2	15 „	58 „	97 „
3	11 „	40 „	65 „
4	14 „	44 „	55 „
5	12 „	64 „	71 „
6*	55 „	100 „	115 „

appeared to be trying to move centrally into the group; but it gave rise to no crouching, scattering or distress calls. By 4 minutes excitement appeared to have subsided, but some of the chicks gave occasional distress-calls. Although these calls then became very infrequent, the group continued to show slight signs of being disturbed: there was less pecking and scratching, and the chicks were quieter than before the models started moving. At the end of 15 minutes the chicks were scattered by waving a piece of hardboard overhead. This provoked an outburst of distress-calls which ceased as soon as all chicks had grouped again: that is, after about 20 seconds. During the time they were scattered however, one model passed by, and those chicks which were very close to it, or across its track, took slight evasive action: they "ducked" and ran a few paces away, running from the model rather than towards the other chicks. In the second 15-minute period of observation, the general behaviour of the chicks had not noticeably changed. At no time, in either period, did any of the birds show strong fear of the model, or, on the other hand, signs of following it. Finally, at the end of 45 minutes, the birds were scattered a second time, with exactly the same results as before.

These observations, like those of Collias (1952) all show that distress in the experimental situation is the outcome, in the main, of the isolation of the chick from its companions. Once they have come together the chicks show none of the behaviour patterns which have been called "emotional," and which are characteristic of socialised chicks tested individually, in which they persist for the whole period of the test. And since the individuals of a group stick very closely together and rapidly reform when scattered, it is difficult to suppose the social response in these socialised chicks of being "satiated." Furthermore, exposure of a group of chicks to a strange model, while producing only a very few signs of distress or fear, nevertheless does not stimulate the chicks to follow that model, the tendency being, presumably completely opposed by the attraction which the chicks have for one another. Finally, it may be noted that a single chick is more quickly attracted to a group of several other chicks than to a single one: compare the speed with which chicks responded in Tests 1 and 2b. The greater volume of "twittering's," the greater mass and greater amount of movement of a group presumably provides stronger stimulation than does a single chick.

Discussion

It is evident that communally reared chicks behave as if they were imprinted on one another. Whether the learning involved is essentially similar to imprinting or not, the results, at any rate, would appear to be closely comparable. One consequence of this process is that the post-hatching period of responsiveness to a strange moving object is shortened, so that the "critical period" itself must be reduced. Although strange objects may then be avoided rather than followed, this is a secondary consequence of the effect of the socialisation and not the principle or primary factor limiting responsiveness. By inference one may then suppose that imprinting on the parent bird would also influence the duration of the critical period. Fear would seem to exert a primary effect only on those birds with no prior social experience and, as has been shown, only when they are older.

The stages in the argument are as follows:

1. Completely socialised chicks cease to follow an unfamiliar moving object at an earlier age than do totally isolated ones.

2. The response of the isolated birds does, however, decline with age, later becoming very

difficult to evoke as a result, probably, of increasing fear. In contrast to this, the following-response reappears in socialised chicks which have been isolated for several days, and it is much more readily elicited in these birds than in the totally inexperienced birds, and depends therefore, on previous social experience.

3. This effect seems to be due to the stimulus-generalisation of a response acquired during the earlier period of socialisation, a conclusion supported by the fact that a similar generalisation occurs in chicks initially exposed to one model, then isolated, and later tested with a second and unfamiliar model.

4. Whereas non-following in totally isolated chicks seems to be mainly associated with the development of strong fear of the moving object, that of socialised chicks is not. Although the latter may avoid the model, sometimes persistently, this behaviour is generally less strong than in the former. On the other hand, these socialised birds are characterised by more persistent searching, distress-calls and other forms of emotional behaviour which are the direct consequence of isolation from their companions. There is no indication that the following-response is reduced in strength by socialisation, for the attraction the chicks have for one another remains very strong. It is relevant to note here that the following-response of young imprinted coots is virtually inexhaustible except by physical fatigue (Hinde, Thorpe & Vince, 1956).

The effects of socialisation are not, therefore, easily explained by the drive-satiation hypothesis. On the other hand it seems that the following-response ceases to be elicited by a strange moving object as soon as the chick has already learnt to follow one object—which may be another chick—sufficiently well to be able to discriminate between this and other objects. This effective stage of socialisation is already reached by the age of 72 hours (Guiton, 1958). At this age, however, fear is not yet sufficiently well developed to prevent a totally inexperienced chick from following a strange object. Fear only begins to interfere seriously with the response 24 hours later. The inhibitory effects of socialisation on the following-response to unfamiliar objects thus take place considerably earlier, so that the development of fear does not seem to be the primary factor which determines the age at which the response is lost except in completely isolated birds.

Previous studies have shown that imprinting of ducklings to one object later restricts the response to that object (Fabricius, 1951; Ramsay & Hess, 1954); and that ducklings become imprinted to the ducklings they are reared with (Fabricius, 1951; Collias & Collias, 1956). These workers do not, however, appear to have found any evidence that the age at which the following-response to a strange moving object is lost is affected by previous imprinting or socialisation. The termination of this period of responsiveness has been attributed either to increasing fear of unfamiliar objects and situations (Hinde, Thorpe & Vince, 1956) or to emotionality unrelated to previous imprinting (Hess, 1957), or to "an endogeneously conditioned decrease of the internal motivation of the following reaction" (Fabricius, quoted from Hinde, Thorpe & Vince, 1956).

The results, especially of experiment 1, raise a number of questions which are at present being studied. In particular, it would be interesting to know:

1. To what extent following under the effect of stimulus-generalisation can lead to further imprinting; and

2. How far the critical period can be extended by reducing fear in isolated birds; or by increasing the inherent stimulating value of the model.

The answer to these questions will probably reveal to what extent and under what conditions imprinting is irreversible as suggested by Lorenz (1937).

Summary

1. In a previous study of Brown Leghorn chicks it was shown that the following-response to a strange moving object was lost at an earlier age in socially-reared chicks than in isolated ones, but that the response reappeared in the former if they were subsequently isolated for several days. This could mean that the loss of the response was due to a short-term, reversible process—the drive satiation hypothesis; or it could mean that socially-reared chicks learned to respond to one another, as opposed to following other moving objects, but that this response was then generalised under conditions of isolation. Experiments, described in this paper, were designed to examine these two hypotheses.

2. The effect of previous experience on the following-response of 4-5 day-old chicks was studied. The chicks were tested singly. Those with no previous visual or physical experience of moving objects or of other chicks followed a moving object (Model B) better than those reared socially from their second day onwards.

On the other hand, if chicks were allowed only four and a half hours of social contact with one another on their second day and then isolated until tested, their response to Model B was stronger than that of either of the two above groups. Restricted experience of other chicks thus potentiated the later response to a strange moving object. In chicks trained on the second day to follow one object (Model M) for 30 minutes, the response was generalised to a different object (Model B) three days later but only if kept in isolation from one another for these intervening days.

3. Chicks trained to Model M on the second day, isolated for three days and then tested with Model M and Model B simultaneously, responded well to Model M but very little to Model B. It is clear therefore, that the models could be discriminated, and that the strange model was only followed in the absence of the one on which the chicks had been imprinted.

4. Non-following by chicks in the first experiment (see 2 above) was associated in most instances with avoidance of the model, or with "searching" accompanied by distress calls, or with attempts to escape from the test-situation. It is noticeable that although initial avoidance of the model was stronger in isolated chicks than it was in socialised ones, the following-response scores of the former were higher than those of the latter. The socialised chicks were, on the other hand, characterised by more persistent "searching" and "distress." This suggests that the absence of following in socialised chicks is not primarily due to fear of the moving object.

5. Observation of 4-5 day-old chicks in the experimental situation, in groups of six instead of singly, showed that distress and fear only occur because a chick is suddenly isolated from its fellows. The grouped chicks showed no signs of "emotionality"; but nevertheless showed no tendency to follow a model. Their social responses to one another, however, were very strong: as soon as a chick was forcibly separated from the other chicks it started making distress calls until it saw the others and ran towards them. The effect of socialisation is not therefore, to reduce the strength of the following-response but to increase its selectivity.

6. The results support the hypothesis that chicks become imprinted or otherwise conditioned to one another, and as a result are henceforth inhibited from following unfamiliar objects, though this may again become possible after a subsequent period of isolation. Since the initial, unselective response is lost in socialised chicks before fear is sufficiently well developed to interfere with it, it is suggested that, under normal conditions, it is this effect of socialisation which determines, primarily, the age at which the chicks cease to follow a strange object, and the age at which, therefore, imprinting ceases to be possible.

REFERENCES

Collias, N. E. & Colias, E. C. (1956). Some mechanisms of family integration in ducks. *Auk.*, **73**, 378-400.

Fabricius, E. (1951). Zur Ethologie junger Anatiden. *Acta. Zool. Fenn.*, **68**, 1-178.

Guiton, P. (1958). The effect of isolation on the following-response of Brown Leghorn chicks. *Proc. roy. phys., Soc. Edinb.*, **27**, 9-14.

Hess, E. (1957). Effects of meprobamate on imprinting in waterfowl. *Ann. N.Y. Acad. Sci.*, **67**, 724-732.

Hinde, R. A., Thorpe, W. H. & Vince, M. A. (1956). The following-response of young Coots and Moorhens. *Behaviour*, **11**, 214-242.

Jaynes, J. (1956). Imprinting: the interaction of learned and innate behaviour: I. Development and generalisation. *J. comp. physiol. Psychol.*, **49**, 201-206.

Jaynes, J. (1957). Imprinting: the interaction of learned and innate behaviour: II. The critical period. *J. comp. physiol. Psychol.*, **50**, 6-10.

Lorenz, K. (1937). The companion in the bird's world. *Auk.*, **54**, 245-273.

Ramsay, R. O. & Hess, E. (1954). A laboratory approach to the study of imprinting. *Wilson Bull.*, **66**, 196-206.

Verplank, W. S. (1955). An hypothesis on imprinting. *Brit. J. anim. Behav.*, **3**, 123.

Weidmann, U. (1956). Some experiments on the following and flocking reaction of Mallard ducklings. *Brit. J. anim. Behav.*, **4**, 78-79.

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THE EFFECT OF NEST BUILDING ON LATER REPRODUCTIVE BEHAVIOUR IN DOMESTICATED CANARIES

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Introduction

The various stages in the reproductive behaviour of birds are performed in a more or less fixed sequence. The question therefore arises, to what extent does the appearance of each stage in the sequence depend on the occurrence of the preceding one? In particular, there is some evidence that nest-building affects later reproductive behaviour. Harper (1904) showed that ovulation in pigeons may be delayed in the absence of appropriate nesting facilities, and Lack (1933) found that differences between the times of egg-laying at colonies of Arctic Terns (*Sterna macrura*) were correlated with nesting conditions. More recently Lehrman (1958) has shown that incubation in doves (*Streptopelia risoria*) depends on the previous occurrence of some nest-building activity.

In this study the effects of nest-building behaviour and the construction of a nest on subsequent reproductive behaviour in the domesticated canary were assessed.

Material and Methods

(1) *Stock*. The canaries used, of the Border variety, were obtained from dealers in the early spring of 1958. Their previous histories were unknown, but most were believed to be first-year birds.

(2) *Procedure*. All birds were placed in pairs in the experimental cages on March 19th. Twenty-four pairs were placed in enamelled metal cages 110 cm. × 35 cm. × 30 cm. as described elsewhere (Dunnett & Hinde, 1958). Six pairs were placed in cages constructed wholly of ½" mesh galvanised wire netting in the form of a vertical cylinder with a flat top and hemispherical bottom. The distance from the top to the centre of the round bottom was about 48 cm. These cages were of approximately the same volume as the enamelled metal cages, but were designed so that no corners or crevices could provide stimuli similar to those provided by a nest-cup. Food and water was provided from hoppers or drinkers flush with the vertical walls. Two cross perches were present.

The birds were divided into groups as follows:

Group I. Kept in enamelled metal cages. Provided continuously with a standard plastic canary nest-pan, 10·5 cm. in diameter and 4·5 cm. deep, which was lined with a little thin felt so that material placed in it did not easily blow out. Superabundant nest-material (approximately equal quantities of dried fine grasses in lengths of about 6 cm., and the body feathers of domestic pigeons) was continuously present, and the birds were permitted to build nests undisturbed. (Initially eight pairs, but one female died soon after the start of the experiment, and another "pair" proved to be two males.)

Group II. Conditions as for Group I except that the nest-pan was not lined with felt, so that most of the material placed in it blew out again as the bird left. Further, any material which did accumulate in the pan was removed at least three times a day. Thus these birds could show nest-building behaviour but could not build a nest (eight pairs).

Group III. Kept in the enamelled metal cages and provided continuously with an unlined nest-pan. Nest-material, in the form of two square wire-netting boxes of side 8 cm., one containing grass and the other feathers, was provided for the duration of three half-hour watches each week. After each watch, all material was removed from the cage, including the nest-pan. Here birds could perform nest-building movements in the nest-pan at any time, but full nest-building sequences were possible only during the thrice weekly watches. (Initially eight pairs, of which one proved to consist of two females which laid on the same day, and one of two males. Data from the female/female pair were included in the analysis of egg-laying dates, but not elsewhere.)

Group IV. Kept in the round-bottomed cages and provided with material only for the duration of the three half-hour watches weekly. Thus these birds differed from Group III in that those stimuli characteristic of the nest-cup, which normally evoke nest-building movements, were not available (six pairs).

All birds were watched with material for at least three half-hour watches per week, between 09.00 and 13.00 hrs. G.M.T. Watches started on March 22-24th and finished for each bird when incubation started, or on June 13th. Nest-building behaviour was recorded, with the use of suitable symbols, on graph paper with a time scale previously marked on it ($\frac{1}{2}'' = 10$ secs.). In addition, a number of watches were made on Groups III and IV when no material was present.

(3) *Data recorded.* The effect of the differences in group treatment on the following aspects of reproductive behaviour were assessed:

(i) Nest-building behaviour. There is no one characteristic of nest-building behaviour which can be used as an index of the intensity of the whole: the criteria used here (number of carryings or placings per watch, median bout lengths of various activities, etc.) are based on a previous study (Hinde, 1958), where the relations between these and other characteristics are discussed.

(ii) Courtship feeding and copulation. These were recorded during the routine watches. The criteria of occurrence were the same as those used in Hinde (1958).

(iii) Egg-laying. All cages were inspected daily for eggs. Although intra-group individual differences in the date of egg-laying were considerable, there were also clear differences between groups. These inter-group differences could not be assessed statistically because the external climatic conditions fluctuated: a day's delay in egg-laying may be more significant if the temperatures were high than if they were low.

(iv) Incubation. Eggs were normally removed 4-5 days after the first egg of the clutch was laid. The prior occurrence of incubation was recorded.

The reproductive cycles of the birds in some groups were delayed as compared with birds in others. It was thus necessary to compare the behaviour of the groups at fixed points in the reproductive cycle. Comparisons were therefore made between behaviour shown at standard intervals before the laying of the first egg. Apart from differences in environmental variables (e.g. temperature) other than those involved in the group treatments, this is not a wholly satisfactory procedure for equating internal state: the first egg may or may not be incubated (p. 40), and may or may not be followed by further eggs (p. 40), and these alternatives may be foreshadowed in behaviour some days earlier (p. 40). It is however, the best method available.

Differences in Building Behaviour Between Groups

(1) *Comparison between Groups I and II.* The building activity of Group II birds, which were not allowed to construct a nest, was greater than that of Group I birds. Thus the mean number of placings per watch on days —6 and —7 was greater in Group II (mean 9·6, range 3-20) than in Group I (mean 4·3, range 1-17). Since these records were taken at similar intervals before egg-laying, the difference here is unlikely to be due to the pre-treatment precocity of the Group II birds (see p. 39). This result is in conformity with the known effect of a reduction in cup size in depressing building activity (Hinde, 1958, p. 32), for the Group II birds were not permitted to complete nests inside their nest-pans.

(2) *Comparison between Groups I/II and Group III.* During the watches with material the Group III birds showed a mean of 19 placings range 8-37) on days —6 to —7 —considerably greater than both Group I and Group II. The high building rates during these watches were undoubtedly associated with the preceding deprivation, and fell off towards the end of each watch. There was a further difference from Groups I and II in that the carrying and, to a less extent gathering, bouts tended to be longer in Group III when watches with similar numbers of placings are compared. Table I shows the median bout lengths of gathering, carrying and sitting for all watches in which the number of placings were 1-5 and 11-15. A similar difference between birds with material constantly and birds provided with material only during watches was found previously (Hinde, 1958).

Outside the thrice weekly watches with material, the Group III birds visited the nest-pan relatively infrequently. This is shown in Table II, which summarises the number of sitting bouts in which building movements were made by Group III birds in watches with no material. The total stimulation they received from the nest pans was thus less than that of Group I or II birds.

(3) *Comparison between Groups III and IV.* During the watches with material, Group IV birds showed two phases of nest-building behaviour. In the first, the stereotyped movements normally performed in the nest-cup were absent, and the behaviour was characterised by long carrying bouts in which the birds made short flights up from the perches with material. Later they placed material at the end of a perch against the wall, or on the floor of the cage, and some-

Table I. Median Bout Lengths of Gathering, Carrying and Sitting in Groups I, II and III when Number of Placings per Watch was 1-5 and 11-15. All early watches, before vigorous building started, excluded, even if number of placings was 1-5; and all watches after start of incubation excluded.

No. placings per watch	Group	Cage no. (& no. watches)	Median bout-lengths (No. bouts)		
			Gathering	Carrying	Sitting
1-5	I	1 (9)	26 (67)	9 (22)	16 (16)
		17 (1)	11 (8)	19 (5)	36 (4)
		26 (3)	6 (13)	6 (13)	66 (4)
	II	3 (8)	19 (80)	14 (50)	15 (21)
		9 (8)	24 (77)	7 (41)	18 (10)
		18 (1)	23 (11)	12 (7)	18 (5)
		27 (4)	13 (26)	11 (22)	16 (10)
		30 (2)	31 (11)	6 (6)	19 (4)
		37 (3)	15 (14)	3 (10)	10 (10)
		44 (4)	38 (11)	4 (9)	34 (6)
	III	25 (2)	19 (38)	20 (30)	26 (9)
		33 (4)	32 (45)	12 (28)	71 (14)
		30 (1)	35 (14)	13 (11)	37 (4)
		46 (1)	27 (17)	37 (14)	8 (5)
11-15	I	26 (4)	19 (52)	5 (54)	16 (51)
	II	3 (2)	23 (45)	4 (36)	22 (20)
		9 (3)	20 (55)	4 (52)	11 (36)
		18 (3)	14 (60)	4 (47)	11 (30)
		27 (3)	12 (50)	4 (46)	19 (36)
		30 (4)	23 (53)	5 (48)	15 (47)
		37 (1)	24 (19)	3 (14)	10 (15)
	III	2 (3)	26 (45)	4 (38)	56 (34)
		4 (1)	26 (22)	12 (18)	12 (11)
		25 (2)	12 (28)	16 (26)	13 (13)
		33 (1)	29 (20)	13 (18)	20 (14)
		43 (5)	23 (110)	10 (86)	10 (39)
		46 (2)	14 (45)	10 (44)	12 (29)

Table II. Number of Sitting Bouts (including Bouts of Those Nest-building Movements Normally Performed in the Nest-pan) Shown by Birds in Groups III and IV when No Material was Present. Each figure in the two right-hand columns refers to one watch with no material. The intensity of nest-building behaviour is shown by the number of carrying bouts shown in a watch with material on the same day, or by the mean number of carrying bouts shown in watches with material on preceding and succeeding days.

Material present		No material present	
Number of carrying bouts	Equivalent number of sitting bouts (Group III)	Number of sitting bouts in individual watches	
		Group III	Group IV
1-10	0-10	0, 0	0, 0, 0, 0, 0, 0, 0, 0, 0, 1
11-20	5	24	0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 0, 3
21-30	10-27	2, 3, 6, 0, 3, 2, 4	0, 0, 0, 3
31-42	26-39	2, 2, 5, 0	0

times performed nest-building movements there. Each individual always placed in approximately the same place in the cage, or in one of two places.

The earlier phase is illustrated by a comparison between the median bout lengths shown by birds in Groups III and IV in Table III. To equate the internal state so far as possible between the groups, comparisons were made for all watches on days —9 to —8 and days —5 and —4 before the laying of the first egg. The gathering bout lengths were of the same order in both groups, but the carrying bouts were longer in Group IV than in Group III. The only exception was at Cage RBC 5 four days before egg-laying: this bird was placing and "scrabbling" (a movement normally made in the next cup) frequently on the floor of the cage. Nearer the laying of the first egg, and before later eggs, more of the Group IV birds started to show short carrying bouts and to scrabble on the cage bottom.

Thus the females in both these groups often built throughout the whole of the half-hour watches and the Group III birds received considerable stimulation from the nest-pan. The Group IV birds had no nest-pan and received stimulation of this type only later in the season when they started to perform nest-building movements in situations which would normally be inadequate to evoke them, such as the floor of the cage.

The same conclusion applies during the much longer periods when no material was present. The Group III birds sometimes sat and/or performed building movements in the nest-pan when material was not present, but the performance of building movements by Group IV birds on the bottom of the cage or elsewhere was rare. This is shown in Table II.

During these periods with no material Group III and IV birds often hopped over the floor of the cage in the manner of birds gathering material, carried their own feathers without pulling them out, or tugged at their mates' feathers. Such behaviour is characteristic of birds deprived of material (Hinde, 1958).

Table III. Median Gathering and Carrying Bout-lengths on Days -8 or -9 and -4 or -5 in Groups III and IV. Figures in brackets indicate number of bouts. All watches made on these days are included, except for those on the female-female pair in Group III.

Day with respect to 1st egg	Group	Cage no.	Bout-lengths (No. of bouts)		
			Gathering	Carrying	Sitting
-9 to -8	III	4 2 33	24 (29) 40 (17) 30 (17)	5 (29) 3 (18) 4 (20)	26 (23) 25 (15) 48 (17)
	IV	RBC1 RBC2 RBC5 RBC6	87 (12) 40 (14) 41 (12) 28 (24)	31 (6) 42 (13) 19 (10) 29 (24)	
-5 to -4	III	25 33 43	13 (28) 34 (18) 35 (13)	16 (26) 3 (22) 16 (10)	26 (13) 60 (16) 17 (6)
	IV	RBC1 RBC2 RBC5 RBC6	32 (19) 23 (13) 40 (16) 62 (12)	50 (11) 38 (12) 6 (13) 82 (9)	

Differences in Date of Egg Laying Between Groups

The dates on which each female laid her first egg are shown in Fig. 1.

The birds of Groups I and II laid all their first eggs between 4th and 29th April, with the exception of one bird from Group I which was sickly throughout most of April and laid on May 7th. The median date of the first egg in Group II (12/13th April) was earlier than that of Group I (23rd April), but this difference was probably due to an unfortunate chance distribution of birds between the groups, such that the Group II birds were initially more advanced when paired up. Thus:

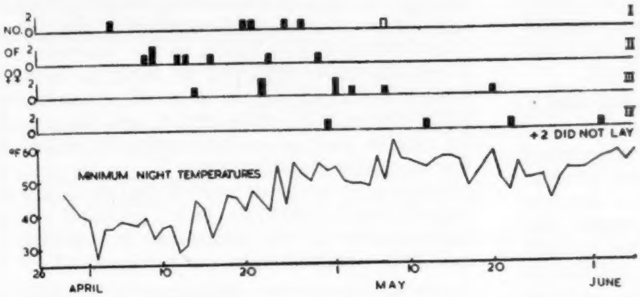

Fig. 1. Dates on which first eggs were laid by birds in Groups I-IV.

(*a*) The Group II birds showed more building behaviour than the Group I birds in the first few days after pairing up. In the early phases of nest-building, canaries gather and carry material but drop it without placing it in the nest: the number of carrying bouts per watch is thus a more useful criterion of building activity than the number of times material is placed in the nest. In the period 20th to 26th March the mean number of carrying bouts per watch was 1·0 (15 watches, range 0-5) for Group I and 2·3 (18 watches, range 0-13) for Group II. At this time so little material was carried to the pan by any bird that the greater activity of the Group II birds can hardly be ascribed to the difference in treatment.

(*b*) The difference between the treatment given to these two groups can only have been effective after building started. In fact there was no noteworthy difference between Groups I and II in the interval between the first day on which placing and sitting were recorded and the day the first egg was laid, the means being 16·0 (range 9-21) and 14·5 (range 9-29) days respectively.

Thus no effect on the date of egg-laying of the removal of material from the nest in Group II, or of the consequent increase in building activity, is demonstrated by this result.

Group III birds laid their first eggs between 14th April and 20th May. The median date was 1st May, and 5 out of 8 of them did not lay until all the Group I and II birds (with the exception of the sick one) had laid. Thus the egg-laying of these birds was delayed as compared with Groups I and II.

Only 4 of the 6 females in Group IV laid during the course of the experiment, which was continued up to July 6th. All of these 4 birds laid their first eggs after all the birds of Groups I and II (except the sickly one), the median date for those which did lay being 28th May. Further, 3 of the 4 Group IV birds which laid did not do so until after 7 of the 8 birds in Group III. Thus, the egg-laying of this Group was delayed as compared with all other groups.

Thus, while no effect of the differences in treatment between Groups I and II on egg-laying is demonstrated by these data, laying was delayed considerably in Group III and even more in Group IV. Since it is nest-building which is affected most immediately by the group treatment, the effects on nest-building are probably primary, the differences in egg-laying date resulting from them. A likely factor here is the extent to which the groups were subjected to stimulation of the type normally presented by the nest-cup (see p. 36). This view is rendered the more probable by the fact that stimuli from the nest-cup are known to produce a decrease in building behaviour.

The data presented above showed that the birds in Group II visited the nest-pan more often than those in Group I. Since there is no obvious difference between these groups in the median sitting bout length (Table I) they must have spent more time sitting in it (see also Hinde, 1958, p. 34). However, although Group II did lay a little before Group I, it was not considered that this difference was due to the treatment. The absence of any effect on egg-laying date, however, would not be incompatible with the view that stimulation from the nest-cup is important in determining the differences in date of egg-laying. The bare nest-pan could provide sufficient stimulation, so that the egg-laying of the Group II birds was not appreciably delayed under these conditions. Alternatively, the more frequent visits of the Group II birds to the pan could compensate for the smaller cup size of the complete nests of the Group I birds, so that the effective stimulation is similar in both groups.

The possibility that it is the overall reduction in time spent in any form of nest-building behaviour which causes the delay in egg-laying seems improbable, since the Group III and Group IV birds had material for the same period (three half-hour watches per week) and spent nearly the whole of these watches in building activities. The essential difference between

Groups III and IV would seem to be the availability of the stimuli from the nest-cup, and that between Groups III and I/II to be the frequency with which these stimuli were encountered.

Differences in Other Reproductive Activities Between Groups

(1) *Courtship feeding*. The mean frequency of courtship feeding during watches with material in the ten days preceding the laying of the first egg is shown in Table IV. For this purpose two eggs laid less than three days apart were counted as a clutch. Courtship feeding was less common in Group II than in Group I, and still less frequent in Groups III and IV. These differences may be merely a consequence of the differing amounts of building activity shown during the watches, since Group II placed more often than Group I, and Groups III and IV spent more time building during the watches with material than did the other groups.

Table IV. Mean Number of Courtship Feedings per Watch in the 10 Days Before the Laying of the First Egg

	Group I	II	III	IV
No. of watches	47	53	55	19*
Mean no. of courtship feedings per watch	0·60	0·32	0·15	0·16

*The data refer to first and later clutches from Groups I-III. Since Group IV laid eggs irregularly and not in clutches, it was only possible to use the data for the ten days preceding the first egg. However, in 67 watches made on or after the tenth day before the first egg, the four birds which did lay showed courtship feeding on an average 0·11 times per watch. Courtship feeding of the two females which did not lay was never seen.

(2) *Laying of clutches as opposed to single eggs.* When a bird in Groups I, II or III failed to incubate, its eggs were removed 4 days after the first one was laid, and the bird was allowed to go on to another cycle of nest-building and egg-laying. The eggs laid by Group IV birds invariably dropped through the bottom of the cages. The frequency distribution of the intervals between successive eggs laid by birds in Groups I-III shows a peak at one to two days caused by successive eggs in a single clutch, and indications of another peak at seven to twelve days caused by successive clutches (Table V). In Group IV the first peak is absent and the eggs were laid at rather irregular intervals. This is probably also a consequence of the reduction in stimulation normally obtained from the nest-cup.

(3) *Incubation.* No differences in incubation behaviour between Groups I, II and III were apparent. In each group approximately half the females incubated their first clutch (3/6 birds in Group I, 4/8 in II, and 5/8 in III).

Those birds which did not incubate their first egg or clutch almost all incubated later; it is not known why they failed to do so the first time. First eggs laid early in the season were apparently less likely to be incubated than those laid later: in Groups I and II only one out of 4 first eggs laid before 10th April were incubated, compared with 6 out of 9 laid later in April. Copulation is equally frequent in cycles leading to incubation and cycles which do not, but courtship feeding is significantly more frequent in the former (Table VI). This suggests that the internal state of the female some days before the first egg is laid may be different in cycles leading to incubation from that in cycles which do not. Since egg-laying is sometimes not followed by incubation, and since incubation sometimes starts before egg-laying, and occasionally occurs without it, the control of incubation and egg-laying (but not necessarily ovulation) must be to some degree independent.

None of the Group IV birds which laid eggs showed incubation behaviour. Since the eggs dropped through the bottom of the cage, lack of incubation may have been due to lack of

Table V. Frequency Distribution of Intervals Between Successive Eggs

Group	Intervals between successive eggs (days) 1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	>16
I	5	1				1			3
II	8	1	1		5	1	2	1	4
III	7	1		3	2	3	1		
IV	1	1	3	2	2		1		1

Table VI. Frequency of Courtship Feeding and Copulation in 10 days Preceding Laying of First Egg. All Groups

	Clutches not followed by incubation	Clutches followed by incubation
Number of watches	48	107
Frequency of courtship feeding per watch	·10	·45
Frequency of copulation per watch	·17	·17

appropriate external stimuli. However, some of these birds performed the stereotyped movements of nest-building behaviour on the floor of the cage, and could presumably have adopted the incubation posture there.

Conclusion

The reproductive cycle in birds depends on internal changes set in motion by external factors (changes in day length, temperature, etc.) acting through a sensory-hypothalamic-pituitary mechanism (e.g. Rowan, 1926; Marshall, 1954). The successive phases of the cycle, however, do not then follow automatically—each depends on further stimuli from the environment and/or further internal changes. The female may lay eggs without going through all the earlier phases of reproductive behaviour, but egg-laying is then delayed and clutch size is abnormal. For biologically successful reproductive behaviour, nest-building activities and a complete nest are essential.

Summary

1. Domesticated canaries were subjected to various degrees of deprivation of nest-material and nest-site in order to assess the effects of nest-building activity and the construction of a nest on later reproductive behaviour.

2. All birds were watched with nest-material for half an hour three times a week. Those groups which were deprived of material between these watches were also observed occasionally at other times.

3. Those birds which had material continuously, but were not permitted to construct a nest, built more actively than those allowed to build undisturbed. Birds without material for most of the time built vigorously during the watches with material, but seldom visited the nest-pan at other times. Birds without a nest-pan showed active building behaviour but it was mainly limited to the early phases of the nest-building sequence.

4. Egg-laying was delayed in the birds deprived of material, and even further delayed in those deprived also of a nest-pan. This was probably because stimulation from the nest-pan during building normally accelerates egg-laying.

5. The effects of the treatment on courtship feeding, the laying of clutches as opposed to single eggs, and incubation behaviour are also discussed.

REFERENCES

Dunnett, G. E. & Hinde, R. A. (1957). Chapter on other Passerine species in *U.F.A.W. Handbook on Laboratory Animals*. London: U.F.A.W.

Harper, E. H. (1904). The fertilisation and early development of the pigeon's egg. *Amer. J. Anat.*, **3**, 349-386.

Hinde, R. A. (1958). The nest-building behaviour of domesticated canaries. *Proc. zool. Soc. Lond.*, **131**, 1-48.

Lack, D. (1933). Nesting conditions as a factor in controlling breeding time in birds. *Proc. zool. Soc. Lond.*, **231-237**.

Lehrman, D. S. (1958). Induction of broodiness by participation in courtship and nest-building in the ring-dove (*Streptopelia risoria*). *J. comp. Physiol. Psychol.*, **51**, 32-36.

Marshal, A. J. (1954). *Bower Birds*. Oxford University Press.

Rowan, W. (1926). On photo-periodism, reproductive periodicity, and the annual migration of birds and certain fishes. *Proc. Boston Soc. nat. Hist.*, **38**, 147-189.

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BRENT GOOSE *(Branta bernicla* (L.)*)* WINTER FEEDING PATTERN AND ZOSTERA RESOURCES AT SCOLT HEAD ISLAND, NORFOLK

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Introduction

This paper describes work done in 1955-1958 on the feeding habits of Brent geese wintering in the Scolt Head Island Nature Reserve, Norfolk. The work was planned to find out if the *Zostera* food resources were adequate for the geese or if grazing was seriously reducing the *Zostera*. When it was found that the food habits of the birds were more varied than expected, it was decided that a study of the seasonal feeding pattern of the birds in more detail by regular field observation of their movements and by analysis of their droppings, would be worth while.

Historical Background

Wildfowlers and other bird watchers have frequently reported that *Zostera* is an important food of Brent geese in winter. Interest in the Brent goose was stimulated during the early 1930's when a "wasting disease" wiped out much of the *Zostera* occurring in extensive beds on European coasts and also on the Atlantic coasts of North America. The causes of the "wasting disease" are obscure, but the evidence suggests that a mycetozoan parasite *Labyrinthula* sp. was associated with the "disease" and for some unknown reason became especially active on North Atlantic coasts in 1931-2 (Cottam & Munro, 1954). Butcher (1941) reported that a decline in *Zostera* was noted on British coasts in 1920-22, though the greatest decline was in 1931 and 1932. In this country, *Zostera* was further reduced in amount, especially on south and east coasts, by the very rapid spread of *Spartina townsendii* H. & J. Groves on to the higher lying *Zostera* beds. In Norfolk and Essex the active spread of *Spartina townsendii* on to *Zostera nana* Roth and *Z. hornemanniana* Tutin areas is still going on.

The latest information on the recovery of *Zostera* beds (Cottam & Munro, 1954) shows that there has been a marked improvement in many areas especially in recent years. In Europe the best recovery of *Zostera* is said to be in the English Channel area. At Langstone Harbour, in Hampshire, for example, both *Z. nana* and *Z. hornemanniana* are actively colonising ground in shallow creeks from which they were absent a few years ago (Westrup, *in litt.*).

Cottam (1935) noted that American pale-breasted Brent geese (*Branta bernicla hrota* (Müller)) were actually increasing before the "disease" affected *Zostera*. Numbers had reached more than 250,000 birds before the 1930's, but had dropped to about 22,000 by 1935. Since 1935 there has been a recovery in numbers of American Brents and Cottam & Munro (1954) estimate that numbers in 1954 were again about 250,000. At Terschelling, West Frisian Islands, Holland, Brent geese were formerly at least three times more numerous than at the present time (maximum population 2,000), according to Morzer Bruijns (1955).

There is little information about numbers of Brent visiting the British Isles before or immediately after the onset of the *Zostera* disease. The only conclusion that can safely be drawn from the evidence is that numbers of Brent fluctuate widely from year to year in individual estuaries. There is some evidence that suggests that numbers of Brent visiting the British Isles are partly dependent on the severity of the winter. Chapman (1889) and recently Parish (1953-4) have pointed out that winters in which large numbers of Brent appear on the British coast are usually severe and may coincide with a freeze-up of the Baltic Sea.

Food of Brent

Campbell (1946) examined 12 stomachs from the Blackwater Estuary, Essex, and one from Sussex. *Enteromorpha* and *Zostera* (probably *Z. nana* and *Z. hornemanniana* from leaf measurements given) were the main foods in five of the stomachs from Essex and in the one from Sussex. Grasses, including *Festuca rubra* L. were the main foods in three of the stomachs from Essex. Small quantities of other algae, leaves of *Halimione portulacoides* (L) *Aell*, and seeds of *Armeria maritima* (*Mill.*) *Willd* occurred. One stomach from Essex contained over 40 *Hydrobia ulvae* (*Pennant*) and about 20 other molluscs not identified. Small quantities of Crustacea, *Idotea*

sp. and *Gammarus* sp. were found and thought to have been accidentally ingested with *Enteromorpha*.

Morzer Bruijns (1955) records that Brent geese at Terschelling fed mainly on *Zostera nana* in autumn but also on *Salicornia*, *Puccinellia*, and *Enteromorpha*. In midwinter when the *Zostera* and *Salicornia* died off, birds fed on *Enteromorpha*. In spring the birds fed on *Salicornia* and *Puccinellia* and were also seen on the highest saltings where *Armeria maritima* and *Festuca rubra* occurred. He states that in most cases the flocks of geese remain constant to one area.

Little is known of the food of European dark breasted Brent geese (*Branta bernicla Bernicla* (L.)) breeding grounds, but Turgarinov (1941) reports that they will feed on mosses and lichens on arrival, and later, in spring, on the young shoots of grasses.

Stomach analyses of American pale-breasted Brent collected before 1932 had *Zostera* as the main food. Analyses made after 1932 showed that algae formed the main food (Cottam *et al.*, 1944).

Lynch (see Cottam *et al.*, 1944, p. 48) examined 45 droppings of pale-breasted Brent in New Jersey in 1936 and found 60 per cent. green algae and 40 per cent. rootstocks of *Spartina* sp. in an area where *Zostera* and *Ruppia* were rare or absent.

The available evidence suggests that Brent geese of all races live on a mainly vegetable diet and that *Zostera* when obtainable is an important part of it. Green algae have been important foods at least since the 1930's and a variety of other plants are taken. Animals, including molluscs, worms, and fish eggs, are occasionally taken by individual birds.

Feeding Behaviour of Brent Geese

Witherby *et al.* (1943) recorded that Brent geese feed on *Zostera* beds when these are uncovered by the tide or covered by shallow water. *Zostera* is pulled up bodily, the roots being preferred, though to some extent the leaves are also eaten. The birds are mainly diurnal feeders but Chapman (1889) observed Brent geese feeding by moonlight. Burton (1957) reports that birds at Foulness, Essex, will feed at all states of the tide. He has observed that feeding habits vary according to the thickness of the plant cover. "In areas of thick *Zostera*, the Brent graze haphazardly, walking fast, and tearing up pieces here and there. Where it is thinner, they stop frequently, and spend some time thoroughly clearing an area of mud, taking rhizomes and everything. Looking at the mud afterwards, these areas can be picked out at once as they are 2 to 3 feet in diameter, and bare. In early autumn, they stand out as depressed regions containing short, bright green regenerated *Zostera*, amongst a general cover of older, dark coloured plants. When the *Zostera* is very thin, they walk straight along, not lifting their heads for long periods, clearing every piece in their tracks." He also notes that "Brent in Essex frequently eat bits of *Aster tripolium* L. when high tide forces them up to the edge of the salting."

Brent feeding on *Enteromorpha* appear to take food cleanly off the mud surface without ingesting much mud. Birds feeding on *Zostera* rhizomes ingest a good deal of mud, and Burton (*in litt.*) suggests they may eat gravel deliberately. This would help to grind up food and may even help to scour the gut free of tapeworms (Cottam *et al.*, 1944, p. 47). Plates I, A. & B, show Brent on the feeding grounds.

The Study Area

Scolt Head Island (Fig. 1) lies just below latitude 53° N. on the North Norfolk coast less than 10 miles from the mouth of the Wash. It is about half a mile wide and about four miles long and its long axis is roughly parallel with the coast. The higher parts of the island are covered by vegetated sand dunes which rest on a base of shingle. Lateral shingle ridges again capped with sand dunes project at intervals from the long axis southwards towards the mainland, and between them are salt marches developed on silt (see Steers, 1948, pp. 358-365). The island is separated from salt marshes adjoining the mainland by Norton Creek which dries in places at

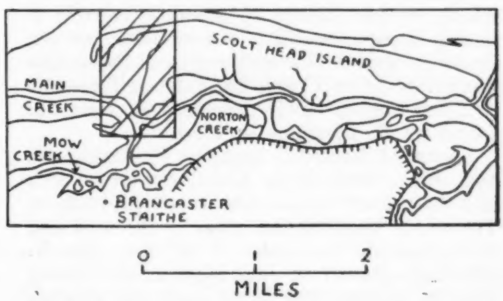


Fig. 1a. Scolt Head Island showing the study area (rectangle shaded diagonally).

low water. A large shallow bay near the western end of the island drains at low water exposing an extensive area of mud flats. This bay is known as the Cockle Bight.

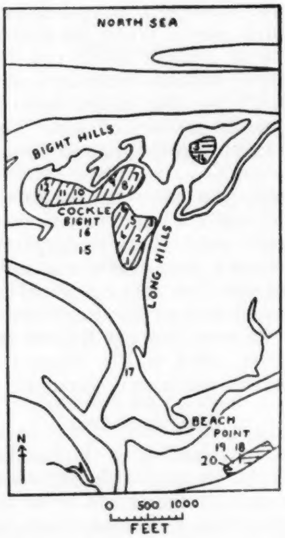


Fig. 1b. The study area showing known distribution of *Zostera* at Scolt Head Island on October, 1955. Diagonal shading shows pure *Zostera nana* areas, horizontal shading shows *Zostera hornemanniana* areas which also contain small amounts of *Zostera nana*. Numbers refer to sampling plots.

Present Food Resources at Scolt

The Cockle Bight is the main site for *Zostera* on Scolt Head Island, and contains about 18 acres (7·3 hectares) of *Z. nana* and about 2 acres (0·8 hectares) of *Z. hornemanniana* (Fig. 1). There are also about 2½ acres (1 hectare) of mixed *Z. nana* and *Z. hornemanniana* on the landward side of Norton Creek near its western mouth. In Mow Creek, less than half an acre (0·2 hectares) of newly developed *Z. nana* was found by R. Chestney in 1956.

About 23 acres (9·3 hectares) of *Zostera* are available to Brent in the Scolt Head Island area and the nearest outside sources are probably at Thornham Harbour five miles to the west and Wells harbour five miles to the east. Mr. R. Chestney, Warden of Scolt Head Island Nature Reserve, reports that Brent from the Reserve occasionally visit Thornham Harbour in hard weather, but for most of the winter they remain in the immediate neighbourhood of the Reserve.

Enteromorpha and other green algae are abundant round the shores of Scolt Head Island and on the adjoining mainland shores. *Puccinellia maritima* (*Huds.*) *Parl.*, *Aster tripolium*, *Halimione portulacoides* and other higher salt marsh plants are also generally abundant. *Zostera* is the least abundant food plant in the area.

Layout of Sample Plots

Plots 20 × 20 yards square were measured out for sampling purposes and these were marked at their corners with polythene tubing pushed on to steel rods.

Seventeen plots were laid out on *Zostera*. Plots 13 and 14 were only 10 × 20 yards and 5 × 20 yards respectively because most of the *Zostera* in this area was on deep liquid mud and only these smaller areas were accessible. Three plots (of full size), Nos. 15, 16 and 17, were also laid out on *Enteromorpha* beds (Fig. 1).

Zostera Cover Sampling by Point Method

The percentage cover of *Zostera* and bare ground was measured by placing a point (4 mm. diam.) 300 times in the plot area and recording whether *Zostera* leaves touched it or not.

The size of the point used over estimates the actual cover substantially (Fig. 2) but the method is rapid to use and quite satisfactory for measuring *changes* in cover which were the primary interest.

Zostera Standing Crop Weight Sampling Method

Some attempt to relate percentage cover results to standing crop weight of fresh green *Zostera* shoots was made outside the plot areas. The method was to lay down a 25 cm. square gridded into 100 smaller squares and estimate the percentage cover with the point placed once in each small square, and in addition, to obtain eye estimates of cover from two independent observers. The sample square was then dug up, the *Zostera* sieved free of mud and taken to the laboratory in polythene bags. The fresh shoots and green leaves were cut off, lightly blotted to remove surplus moisture, weighed fresh, and then weighed again after oven drying at 95°C. Seven of these samples were taken in *Z. nana* and one in *Z. hornemanniana*.

Standing Crop Weight of Zostera Available to Brent at Scolt

It was found that independent observers gave very close eye estimates of cover (± 5 per cent.)

using a gridded 25 cm. square quadrat. The point cover estimates plotted against eye estimates (Fig. 2) show that the point method grossly overestimates the cover as estimated by eye. When

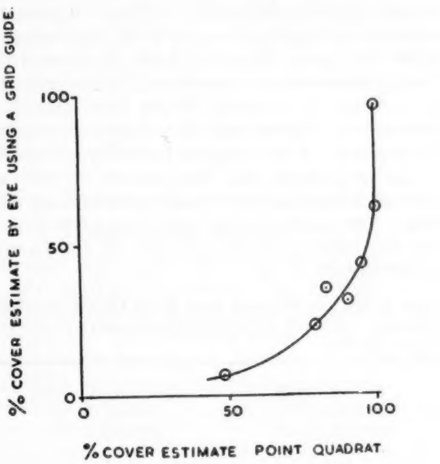


Fig. 2. Approximate relationship between eye and point estimates of *Zostera nana* winter cover—Scolt Head Island, Norfolk.

the eye estimates of cover are plotted against fresh weight of *Zostera nana* (Fig. 3), the graph closely approximates to a straight line passing through the origin. It is concluded in view of this, and the accuracy with which these estimates can be made by different observers, that eye estimates using a small grid would be a better method of assessing the actual *Zostera* cover than the point method. Some estimate of the standing crop of *Zostera* available to Brent geese at Scolt Head Island can be derived from the graphs by taking the average percentage cover of *Zostera* in the sample plots, converting this figure to the actual cover as estimated by eye and reading off the fresh weight. Since there is

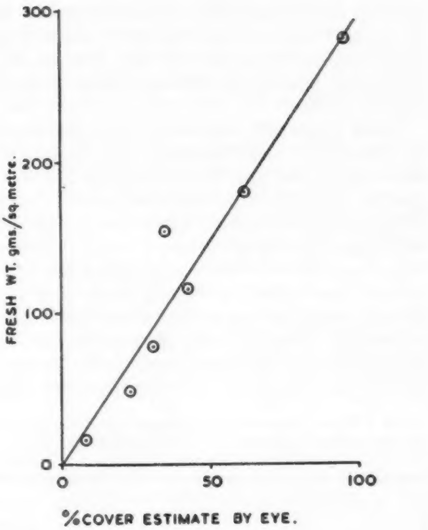


Fig. 3. Regression line showing relationship between eye estimate of cover and fresh weight of *Zostera nana* winter leaves and shoots in gm/sq. metre—Scolt Head Island, Norfolk.

only one sample from *Z. hornemanniana* and the *Z. nana* samples are also inadequate, the result must be considered as very approximate. The figure works out at approximately 12 tons (12·2 tonnes, metric) of fresh green winter leaves and shoots of *Zostera* available at Scolt Head Island in October of each of the two years 1955 and 1956.

Brent Numbers and Movements, and Zostera Changes in the Winter 1955-6

Counts of geese were made by Mr. R. Chestney on 55 days during the winter (see Fig. 4). His observations suggested that the main winter flock of about 200 birds fed in the Cockle Bight

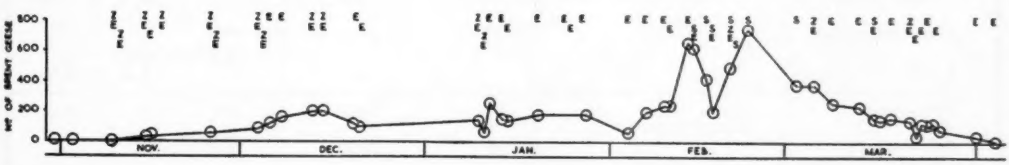


Fig. 4. Brent geese numbers and movements on feeding grounds at Scolt Head Island, Norfolk, in the winter 1955-6.

area on arrival and then worked round by Beach Point to Norton Creek by early January where they stayed for most of the winter. In late February and early March, birds visited the higher marsh.

Birds apparently fed in the main *Zostera* areas in November and December (flocks of 100-200 were seen near the Norton Creek *Zostera* bed on 4th, 7th and 12th December) when the winter leaves of *Zostera* were fresh. Since there is not sufficient *Zostera* in Norton Creek to support the large numbers of birds seen there through the bulk of the winter, it seemed likely that *Enteromorpha* was the main diet from December to February. Finally, the movement to higher marsh in late February and early March suggested that plants of the saltings were taken at the end of the winter. No unusual weather conditions occurred during the winter of 1955-6, except that the month of February was particularly cold.

The *Zostera* and *Enteromorpha* plots were measured in October 1955, before the geese had arrived and again in April 1956, just after the geese had gone. Results (Table I) showed that the October cover values for *Z. nana* plots had been reduced by about 70 per cent. during the winter and that in individual plots as much as 96 per cent. of the original cover had gone. The *Z. hornemanniana* had disappeared entirely and was re-colonising by newly germinating seedlings. *Enteromorpha* had been reduced in amount varying between 20-70 per cent. of the October cover values.

Table I. Point Estimates of *Zostera* and *Enteromorpha* Ground Cover in Sample Plots at Scolt Head Islands, Norfolk, at the Beginning (October) and End (April) of the 1955-6 Brent Goose Season. Losses of *Zostera hornemanniana* were probably mainly due to Wigeon grazing.

Species	Area	Plot No.	17th Oct., 1955 Estimates % ground cover	11th April, 1956 Estimates % ground cover
Z. nana	Cockle Bight South	1	53·4	13·8
		2	87·5	24·4
		3	61·9	31·9
		4	55·6	9·7
		5	65·0	11·9
		6	54·1	24·1
Z. nana	Cockle Bight North	7	81·3	14·7
		8	52·8	9·7
		9	56·3	14·7
		10	76·9	3·1
		11	83·4	9·1
		12	42·5	17·2
Z. hornemanniana	Cockle Bight Pit	13	67·5	7·8 (seedlings)
Z. hornemanniana		14	88·3	29·7 (seedlings Z.H. & Z.N.)
Z. nana			2·5	
Z. hornemanniana	Norton Creek (opposite Beach Point).	18	34·1	0·6 (seedlings, Z.H. & Z.N.)
Z. nana			5·3	
Z. hornemanniana		19	11·3	5·0 (seedlings, Z.H. & Z.N.)
Z. nana			15·6	
Z. hornemanniana		20	26·3	5·3 (seedlings, Z.H. & Z.N.)
Z. nana			2·5	
Enteromorpha	Cockle Bight South	15	84·7	30·3
Enteromorpha		16	78·8	36·9
Enteromorpha	Beach Point	17	89·4	70·0

These results give some idea of the changes occurring during a Brent season. Mr. Chestney observed that Brent rarely visit the main *Z. hornemanniana* bed (Plots 13 and 14). Wigeon have been observed feeding in this area, however, so the losses of *Z. hornemanniana* may be largely due to them. It is likely also that winter losses in *Zostera* are caused by frost and storm wave damage. Nevertheless, the combined action of grazing, frost and wave action had not by any means cleared the *Z. nana* areas completely during the winter.

Brent Numbers and Movements and Zostera Changes in the Winter of 1956-7

Counts were again made by Mr. Chestney on 20 days during the winter (Fig. 5). Birds were seen feeding at all states of the tide and in most cases on the *Enteromorpha* beds. They were not actually seen feeding on *Zostera*, but from the 18th-20th January a big flock of 600-800 birds was seen feeding on *Aster*/*Puccinellia* saltings when high spring tides had covered up the rest of the feeding grounds.

The pattern of seasonal movements of the birds on the feeding grounds during the winter was substantially the same as in the previous winter.

The winter was exceptionally mild and this was probably the reason the birds left a month earlier than in the previous winter.

Zostera and *Enteromorpha* plots were sampled in October 1956 and there was no significant difference in the aggregate amount of *Z. nana* recorded, from the previous estimates of October 1955. There was an overall loss of 13 per cent. in *Z. hornemanniana* plots, however, which was thought to be partly due to silting up in these *Zostera* areas as a result of the spread of *Spartina townsendii*. There was no significant change in the *Enteromorpha* plots.

Plots were resampled in December, at the beginning and end of a week's visit in an attempt to assess the intensity of grazing occurring at that season.

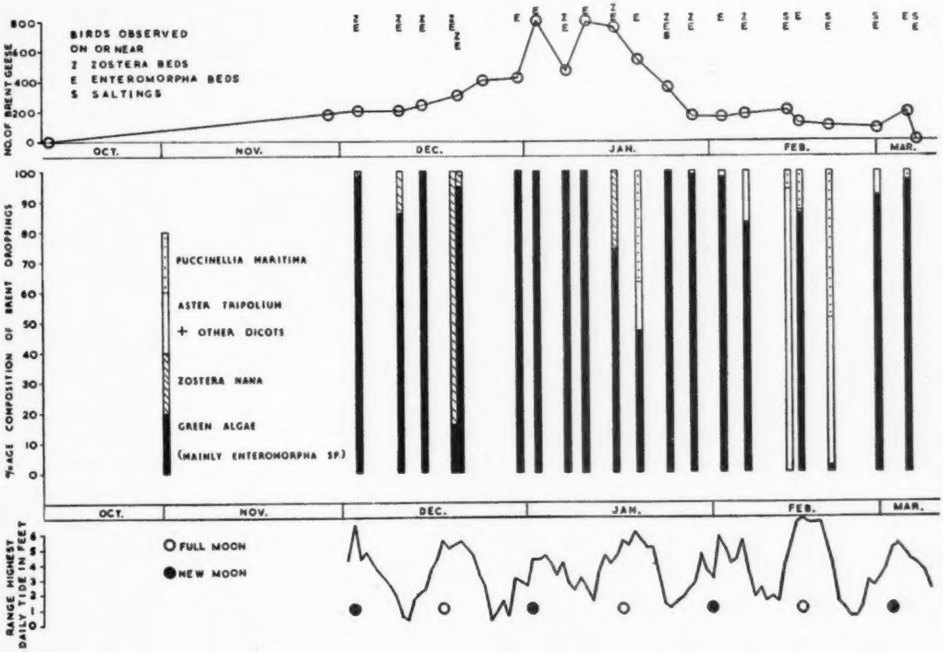


Fig. 5. Brent geese numbers and movements on feeding grounds at Scolt Head Island, Norfolk, in the winter 1956-7, together with the results of dropping analysis on 20 days. The bottom curve shows the range of highest daily tides recorded at Wells, 5 miles to the east of Scolt.

By 14th December, less than a month after the main flock had arrived, a 30 per cent. reduction in *Z. nana* cover and a 75 per cent. reduction in *Z. hornemanniana* cover had occurred. Actual gains had occurred in some *Enteromorpha* plots due to winter growth. On remeasuring the plots at the end of the week's visit in December, Plots 1, 2, and 3 on *Z. nana* had lost a further 18 per cent. of their cover. No significant changes occurred in other plots. There was no severe tidal action or frost during this period and fresh droppings of Brent geese containing *Zostera* were found during the visit, so it seems likely that losses recorded were mainly due to grazing by the geese.

These results again suggested that *Zostera* was eaten mainly during the early part of the winter.

Petrol rationing prevented resampling of plots in the spring, but Mr. Chestney reported on 26th February, 1957, that the *Enteromorpha* had been completely stripped from the plots and from most of the surrounding shores by the geese. By 8th April, regrowth had completely restored the cover. There was still some *Z. nana* winter growth left in the Cockle Bight when the geese left, as in the previous year.

Thus the result of this second winter gave further evidence of a distinctive seasonal feeding pattern of the birds, that *Zostera* was mainly eaten in the early part of the winter and that the *Zostera* resources were not fully used up at the end of the winter.

Brent Numbers and Movements in 1957-8

Mr. Chestney's records of movements on the feeding grounds (Fig. 6) showed again the sequence recorded in the previous two winters, but the geese went on to higher salt marshes in early January, nearly two months earlier than in the previous two seasons and they fed there regularly during most of January and February. Mr. P. Wayre (*in litt.*) noted that the Brent at Blakeney, Norfolk, also took to feeding on *Aster tripolium* and *Puccinellia maritima* on the higher saltings in January when they normally feed on *Zostera* and *Enteromorpha*. This change in behaviour could have been caused by a temporary failure in the *Zostera* and *Enteromorpha* resources due to over-grazing.

A visit in mid-March, 1958, showed that both *Enteromorpha* and *Zostera* resources were much depleted, while food on the higher saltings was generally abundant. Birds were seen feeding on *Enteromorpha*, *Z. nana* and *Aster* during the visit. Very little *Enteromorpha* was left and no *Z. hornemanniana*, but some *Z. nana* was still available in the Cockle Bight.

Analysis of Droppings

As plant fragments could be recognised in the droppings of Brent geese, samples were analysed at least once a week throughout the winters of 1956-7 and 1957-8 in order to follow the feeding, pattern in more detail.

Method

Three or four samples each of 5 to 10 droppings were taken on each sampling date. In the first year 60 samples collected on 20 days were examined. In the second year 109 samples collected on 30 days were examined. At least five sub-samples from each sample were examined.

Each subsample was dispersed in a drop of water by padding with a rubber-tipped glass rod on a microscope slide and examined under a cover-slip at a magnification of 90×.

Plate II A-D show the appearance of typical fragments in the droppings when photographed in their natural state, unstained and in water.

Content of Droppings

Results show (Table II) that the droppings in both years consisted almost entirely of vegetable matter and that green algae (mainly *Enteromorpha* spp.) formed the main constituent in each year. No trace of *Z. hornemanniana* was found in

Table II. Percentage Composition of Total Samples of Brent Droppings for Winters 1956-7 and 1957-8 at Scolt Head Island, Norfolk. (T=Trace only)

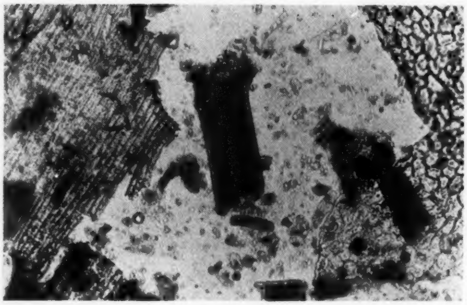
	Vegetable matter	Green algae (thallus)	*Zostera nana* (leaves & rhizomes)	*Aster tripolium* (leaves)	*Halimione portulacoides* (fruits and seeds)	Other dicots. (Mainly *Spergularia marginata*, *Armeria maritima*, and *Plantago maritima*) (leaves & stems)	*Pucinellia maritima* (leaves)	Animal matter
1956-7	100	79	6	10	0	T	5	T
1957-8	100	39	8	15	3	10	25	T

PLATE I

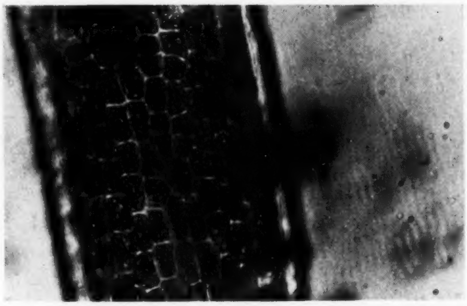
A. Brent geese feeding on mud-flats on the Norfolk coast. *(Photograph by Philip Wayre)*

B. Flock of Brent geese feeding on *Zostera* on the Norfolk coast. Note the thin layer of water on the mud surface which is often characteristic of Brent feeding grounds. On the extreme left is a clump of *Spartina townsendii*, a plant which is invading the *Zostera* feeding grounds at Scolt Head Island and Blakeney, Norfolk. *(Photograph by Philip Wayre)*

PLATE II

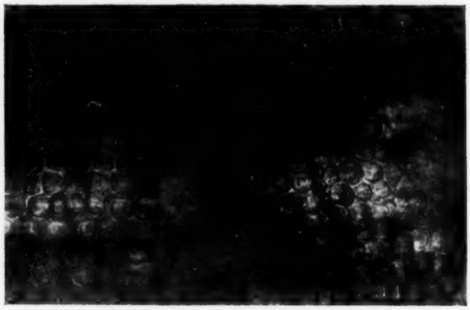


A. Typical sample of plant remains from a Brent goose dropping. On the left is a large fragment of *Puccinellia maritima* leaf tissue. In the centre is a small fragment of *Enteromorpha* sp. On the right is a large fragment *Aster tripolium* epidermal tissue showing stomata. × ·35.



B. Enlarged view of part of the *Enteromorpha* fragment shown in Fig. A. Note good state of preservation of cell contents after passage through gut of Brent goose. × ·180.

C. Typical leaf fragment of *Zostera nana* (showing the full leaf width of *c.* 1 mm.) from a Brent goose dropping. × ·35.



D. Enlarged view of part of *Z. nana* fragment from Brent goose dropping to show the characteristic rounded cells arranged in rows. Compare with Fig. B. × ·180.

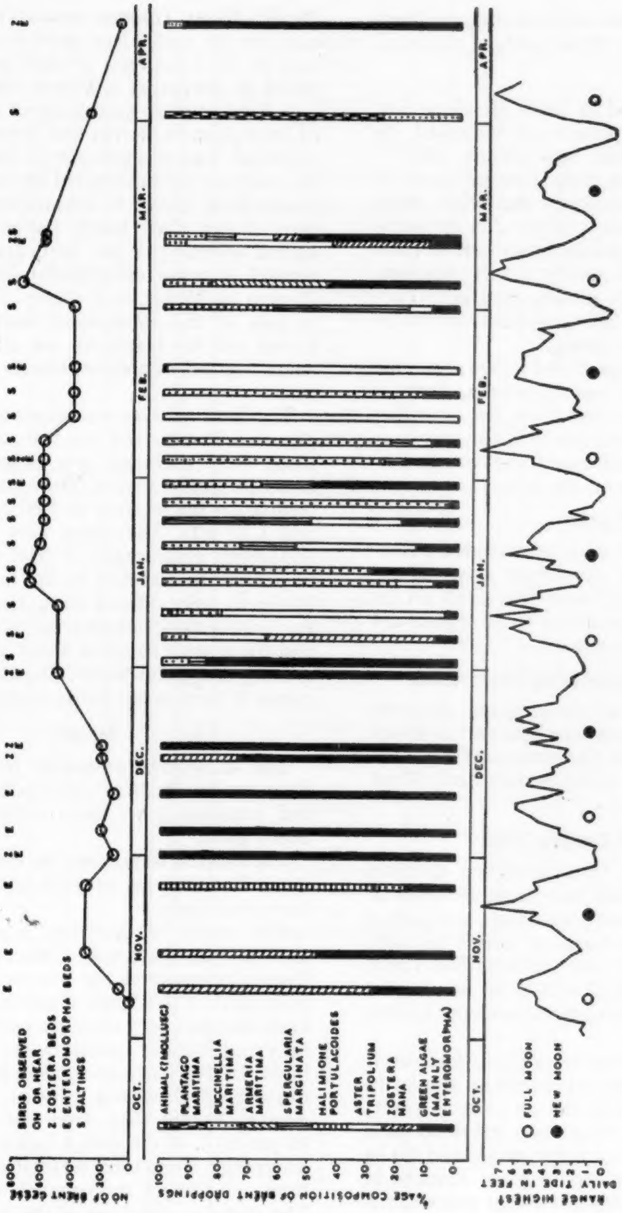


Fig. 6. Brent geese numbers and movements on feeding grounds at Scolt Head Island, Norfolk, in the winter of 1957-8, together with the results of dropping analysis on 28t days. The bottom curve shows the range of highest daily tides recorded at Wells, 5 miles to the east of Scolt.

any sample and *Z. nana* leaf and rhizome fragments formed less than 10 per cent. of the total.

Seasonal Patterns

The results condensed in Table III show that the monthly feeding pattern as indicated by dropping analysis for the two winters, 1956-7, 1957-8, is in accordance with seasonal observations of feeding. *Enteromorpha* and other green algae are main constituents of the diet throughout the winter and especially important in mid-winter. *Z. nana* is taken mainly in early autumn, while higher salt-marsh plants, especially *Puccinellia maritima* and *Aster tripolium*, are taken in late winter and early spring.

The histograms in Figs. 5 and 6 give a graphic picture of the seasonal feeding pattern. There is considerable day to day variation, but nevertheless almost every daily sample in both years contains at least some *Enteromorpha* which emphasises its importance in the diet.

Feeding and the Tidal Cycle

High tides combined with an extended potential feeding period by moonlight seem to encourage the geese to feed most frequently on the higher saltings at full moon for these regions are then least disturbed by man.

Note on Dropping Samples from Other Areas

Dropping samples of Brent geese obtained from two sites in Hampshire and two in Essex (Table IV) suggest that *Enteromorpha* is an important food in other areas besides Scolt Head Island.

Brent Geese Feeding Trial

Conclusions drawn from dropping analyses are open to the objection that the proportions of remnants in the droppings may not reflect accurately the proportions of foods actually eaten. In co-operation with the Wildfowl Trust, Slimbridge, a feeding trial with Brent was carried out to obtain some experimental evidence on this point.

The objects of the trial were (1) to find out if Brent in captivity produced droppings similar to those of wild birds when fed on natural foods; (2) to discover how long food takes to pass through the gut of tame Brent geese, and (3) to find out if the proportions of plant remains in droppings reflect reliably the actual proportions of a mixed feed ingested.

Method

European Brent were not available, so four Pacific Brent (*Branta branta nigricans*) were used for the trial. These were penned on a small area (c. 10 × 15 feet) of close mown turf from which all droppings had been cleared.

A food mixture consisting of chopped leaves of fresh *Zostera marina* and *Aster tripolium* was prepared. The proportions of the two foods in the mixture were estimated by two independent observers by eye in 10 subsamples floated out in petri dishes over graph paper. All estimates agreed within ± 8 per cent. and the result indicated a mean composition of 84 per cent. *Zostera* to 16 per cent. *Aster*. The proportions in two of the subsamples were measured by laying out the fragments on graph paper and results agreed with the estimates within ± 7 per cent.

The food mixture was given to the birds in a pan at 8.30 a.m. and the first samples of droppings were collected two hours later and at intervals until 4.30 p.m. The birds were observed feeding on the mixture at 8.30 a.m., 12.30 p.m., and 1.30 p.m. They were very tame and were apparently encouraged to feed by the presence of people. In addition to the foods mentioned, the birds were offered fresh *Enteromorpha* and *Puccinellia maritima* after the mixed feeding trial and these were eaten in small amounts. Subsequently droppings were collected to see if fragments of these other foods could be recognised.

Results

The droppings collected from the Pacific Brent used in the trial were similar in appearance and consistency to those collected from wild Brent geese.

The shortest time taken for the mixed *Zostera/Aster* feed to pass through the birds was less than two hours.

The results of dropping analysis (Table V) showed that there was a background of grass feeding throughout the trial and without some bulk food of this kind, it seems doubtful if this kind of experiment could be carried out successfully and without upsetting the digestion of the birds. In every dropping sample containing the mixture, *Zostera* was present in substantially greater quantity than *Aster* and when more than 10 per cent. of the mixed feed showed up in the droppings, some trace at least of the *Aster* (less than one-fifth of the original diet) showed up. The mean proportions of the mixed feed showing up in 18 droppings was 91 per cent. *Zostera* to 9 per cent. *Aster* as compared with the mixture of 84 per cent. *Zostera* to 16 per cent. *Aster*

Table III. Percentage Composition of Brent Droppings indicating the Monthly Feeding Pattern for 1956-7 and 1957-8 at Scolt Head Island, Norfolk. (T = trace)

Table III. Percentage Composition of Brent Droppings indicating the Monthly Feeding Pattern for 1956-7 and 1957-8 at Scolt Head Island, Norfolk. (T = trace)

	Green algae (mainly *Enteromorpha*)		*Puccinellia maritima*		*Zostera nana*		*Aster tripolium*		*Halimione portulacoides*		Other dicots. (Mainly *Spergularia marginata, Armeria maritima, and Plantago maritima*)	
	1956-7	1957-8	1956-7	1957-8	1956-7	1957-8	1956-7	1957-8	1956-7	1957-8	1956-7	1957-8
NOVEMBER	—	47	—	3	—	32	—	0	—	18	—	T
DECEMBER	83	95	0	T	17	5	0	T	0	0	T	T
JANUARY	87	24	6	38	4	6	3	21	0	T	T	11
FEBRUARY	57	6	10	46	0	0	33	36	0	0	T	12

Table IV. Brent Goose Dropping Analysis of Samples from Foulness and Blackwater Estuary, Essex, and Langstone and Chichester Harbours, Hampshire, during Winter, 1957-8. (T = trace)

Site	No. samples	Date	Vegetable matter											Animal matter			
			Enteromorpha sp.	*Cladophora* sp.	*Ulothrix* sp.	*Polysiphonia* sp.	*Zostera nana*	*Zostera hornemanniana*	*Aster tripolium*	Other dicots	*Puccinellia maritima*	*Spartina* sp.	Total vegetable	*Hydroidea*	*Copepoda*	Unidentified animal	Total animal
ESSEX	12	9-2-57	93			7	T			T			100	T		T	T
	24	3-3-57	100						T		T		100		T		T
FOULNESS	16	16-3-57	96	1	T		T		T	T	T	3	100			T	T
	4	9-11-57	T				100				T		100	T			T
ESSEX Blackwater Estuary	6	15-2-58	79				21						100	T			T
HAMPSHIRE Langstone Harbour	10	17-11-57	100										100		T		T
	3	4-1-58	100				T						100		T		T
	39	21-2-58	100										100				
HAMPSHIRE Chichester Harbour	2	1-12-57	T				50	50					100				
	4	15-3-58	100				T						100		T		T

Table V. Dropping Analysis Results after Feeding Tame Pacific Brent Geese with an 84 per cent. *Zostera marina:* 16 per cent. *Aster tripolium* Feed at 8.30 a.m. on 21-11-57.

Time	Sample no.	Grass %	Zostera %	Aster %	Zostera as % of Z + A	Aster as % of Z + A
10.30 a.m.	+ D1	97	3	Trace	—	—
	+ D2	100	—	—	—	—
	D3	60	28	12	70	30
12.15 p.m.	D1	37	62	Trace	100	—
	+ D2	100	—	—	—	—
	D3	67	29	4	88	12
	+ D4	100	—	—	—	—
	D5	53	43	4	91	9
	+ D6	100	Trace	Trace	—	—
	D7	45	54	1	96	4
	+ D8	97	Trace	3	—	—
	D9	15	81	4	95	5
	D10	37	57	6	90	10
1.30 p.m.	+ D1	100	—	Trace	—	—
	D2	22	62	14	82	18
	D3	20	77	3	96	4
	D4	17	74	9	89	11
	D5	30	65	5	93	7
	D6	70	30	Trace	100	—
	D7	5	94	1	99	1
	+ D8	97	3	Trace	—	—
	D9	51	42	7	86	14
	+ D10	93	7	—	—	—
3.30 p.m.	D1	49	47	4	92	8
	D2	19	71	10	88	12
	+ D3	100	—	Trace	—	—
	D4	6	82	12	87	13
4.30 p.m.	+ D1	100	—	—	—	—
	+ D2	100	—	—	—	—
	+ D3	90	10	Trace	—	—
	D4	14	78	8	90	10
				Mean	91% Z.	9% A.

+Results ignored as droppings contain at least 90 per cent. grass.

actually ingested, giving an error of $\pm$ 7 per cent. This result supports the assumption that, for the foods given and under the conditions of the trial, food proportions indicated by analyses of droppings gives a good approximation of the food proportions actually ingested.

Enteromorpha, *Zostera marina*, *Puccinellia maritima* and *Aster tripolium*, were eaten by tame Pacific Brent during the trials and these foods were recognisable from fragments in the droppings even when eaten in very small amounts.

Nutritional Analyses

The results in Table VI are derived from analyses carried out by Mr. J. S. Leahy of the Nutritional Research Unit, Huntingdon, to whom our most grateful thanks are due. The results suggest that fresh *Zostera nana* leaves are about three times as rich in protein as fresh *Enteromorpha* thallus, while *Puccinellia maritima* and *Aster tripolium* leaves are intermediate in protein content. Fibre, as estimated by determination of the acid and alkali insoluble material is very low in *Enteromorpha* spp. and there is also relatively little carbohydrate other than algal cellulose. There is unlikely to be much silica in *Entermormorpha*, however, so the ash content will probably consist mainly of mineral nutrients and in this it is relatively rich. There is a higher ash content in *Zostera nana*, but what proportion of this is silica and what proportion mineral nutrient is not known.

Protein determination could not be carried out on the droppings as these would be heavily

Table VI. Nutritional Analyses of Leaf Samples of the Main Brent Goose Foods and of Droppings Derived from Them.
Figures show composition as percentage of the fresh weight.

		Zostera nana	*Puccinellia maritima*	*Aster tripolium*	*Enteromorpha* sp
Moisture	(1) Fresh	74·6	76·6	88·6	93
	(2) Droppings	78·3	82·3	80·3	70·7
Fibre	(1) Fresh	1·38	1·17	1·06	0·33
	(2) Droppings	4·37	2·71	5·89	12·46
Ash	(1) Fresh	4·35	1·85	1·12	2·53
	(2) Droppings	7·67	3·58	8·96	22·92
Protein	(1) Fresh	6·43	3·09	2·30	1·98
Carbohydrate other than cellulose + any material not accounted for by analysis	(1) Fresh	13·14	17·29	6·92	2·16

contaminated with other nitrogenous substances which would give a falsely high protein value.

Fibre in the droppings was contaminated with grit and this will increase both the fibre and ash values above their true values. However, since some attempt was made to collect relatively grit free droppings, the results are probably roughly comparable and suggest that *Enteromorpha* droppings, unlike those derived from the other three foods, contain high amounts of indigestible material.

To sum up, the evidence suggests that *Zostera nana* has high nutrient value, *Enteromorpha* relatively low value except perhaps as a source of mineral nutrients, whilst *Puccinellia* and *Aster* are intermediate in protein content between these two species and probably lower than both in mineral nutrient content.

Discussion

The actual time spent on field work at Scolt Head Island was only 19 days during the period of three years covered by the study. The much more frequent field observations made by Mr. Chestney, Warden of the Scolt Head Nature Reserve, are of great value. Records of this type in which not only bird numbers are given, but also what they are doing, *exactly* where they are, the state of the weather and tide, etc., become significant when supported by studies of food availability and droppings analysis. Campbell (1946) has emphasised the importance of adequate food surveys in understanding the significance of stomach analyses. It is also of great importance to know just how far local flocks range in their foraging. Burton (1957) has noticed that certain flocks can be picked out by a constant size and constant proportion of adult to first winter birds, and that some flocks of Brent move about and mix with other flocks much more than others. Observations suggest that the Scolt flock does remain constant to the area, but further observations on these lines are required. Critical observations of the feeding habits of Brent are not easy to make and the careful description given by Burton and quoted above is an excellent example of what is needed.

A point that emerges from this work is that Brent do not take *Zostera nana* whenever it is available so far as the tides are concerned. This might be due to human disturbance in the Cockle Bight area or it might be that the birds have a real preference for *Enteromorpha*. Whatever the explanation, the fact remains that considerable quantities of *Zostera* were left uneaten at Scolt when the birds were feeding in close proximity to it on *Enteromorpha*, and that some winter growth of *Zostera* was still present when the geese left in spring. The observations suggest that choice of food is determined more by the state of growth at different seasons of a variety of food plants rather than by a special preference for any one of them. The three main types of food, *Zostera*, *Enteromorpha*, and higher salt-marsh plants, are favoured in the diet during the season when each is in its most active growth

phase, autumn, midwinter and late winter to early spring respectively.

The results show also that the diet of British Brent geese is considerably more varied (in the Scolt Head area at least) than is generally supposed. In particular, the importance of *Puccinellia maritima* and *Aster tripolium* in the diet has not hitherto been recognised.

The dropping samples from Essex, together with Campbell's results of stomach analyses (1946, see p. 230), suggest that the feeding pattern of Brent in other parts of the south-east coast of England may be similar to that found at Scolt Head. Observations of wildfowlers and bird watchers, together with our results of droppings analyses from Hampshire harbours, suggest that Brent on the south coast have a much more restricted diet, for they are rarely, if ever, seen on the higher saltings. These saltings are much less extensive than in east coast areas as a result of reclamation and the spread of *Spartina*. They are also more subject to human disturbance. These two factors must restrict the Brent to the more remote *Zostera* and *Enteromorpha* zones.

The remarkably fresh state of preservation of plant fragments in Brent droppings is of great interest. Much of the plant tissue is intact and apparently very little damaged. Sturkie (1954) states that birds digest considerably less crude fibre than mammals, so it may be that they rely principally on mechanical crushing in the gizzard rather than on enzymes to break down cell structure, a process which does not seem to be particularly efficient in the Brent goose. Incidentally Ingram (1933) makes the interesting observation that sheep and cattle grazing on the Islands of Coll and Gunna eat the droppings of geese (principally Barnacle geese) in spring when the surrounding turf is short, and apparently derive considerable nourishment from them.

Nutritional analyses of the fresh foods have given some indication of their relative food value. Owing to contamination with grit, analyses of droppings of *Enteromorpha*, *Zostera*, and *Aster*, cannot really be compared with the fresh foods. However, *Puccinellia* droppings from the high marsh were relatively grit free and these show that proportions of crude fibre and ash in the droppings are very little different from those in fresh *Puccinellia*. This supports the view that these birds digest little crude fibre and rely mainly on mechanical crushing of cells in the gizzard.

The results of droppings analyses are open to the criticism that soft bodied animals eaten would not be detectable in the droppings. Also, proportions of plant remnants in the droppings may not reflect accurately the proportions of plants actually eaten.

There seems to be little evidence from stomach analyses carried out by other workers that animals form a significant part of the Brent goose's diet. However, exceptions have been quoted showing that animals are sometimes taken, and further field observations and stomach analyses are needed.

The second criticism, concerning relative digestion efficiency for different plants also requires further study.

Our own results using tame Pacific Brent were encouraging, however, and certainly lent support to the view that intake food proportions and remnant proportions in the droppings are reasonably closely related though of course this may not be so in wild birds. It was particularly encouraging to find that birds of this type with highly developed social behaviour should be amenable to the condtions of the experiment and that their digestion was not apparently upset by it. Storey (1957) has noticed that in his collection of pink-footed, white-fronted and greylag geese that, "there was a considerable difference in the stools of the captive birds from those in the wild state . . . greylag (and two Canada) geese who were free winged and flighted round the countryside produced stools much closer resembling the natural droppings than their pinioned fellows although they frequently took most (if not all) of their feed in the field where the collection was kept." Storey also noticed that there was a difference in composition of droppings during different seasons and particularly during hard weather and immediately preceding hard frosts.

Results of the droppings analyses taken in conjunction with the field observations of the feeding habits of the birds at Scolt, point strongly to similar conclusions about the seasonal feeding pattern of this flock. This fact, together with the experimental evidence, certainly strengthens the view that analysis of droppings on the lines carried out can give a reliable indication of the food actually eaten by Brent geese. If further evidence can be gained supporting this assumption, dropping analysis should prove a valuable tool in further investigation of the feeding habits of these, and other birds. Beyond occasional observations of actual

feeding, our knowledge of Brent food in this country depends on a total sample of 28 birds' stomachs. Only 13 of these stomachs were taken from Brent on the English coast. The dropping samples from Scolt and elsewhere, even though they may not reflect with great accuracy the proportions of different food actually ingested, do seem to indicate the chief food plant taken at any time, and the total of over 250 samples must have come from at least 300-400 birds.

Finally, it is worth pointing out that this approach allows a good deal of information to be obtained about feeding without killing any birds and has the additional advantage that the same flock can be sampled again and again with minimum disturbance to the birds.

Summary

1. Fluctuations in numbers of Brent geese in relation to their food supply is discussed.

2. At Scolt Head Island, Norfolk, *Enteromorpha* species are the main food of Brent geese, and *Zostera nana*, although locally abundant, is not always eaten when the tides make it available.

3. Study of feeding habits supplemented by analysis of food remains in the droppings of the geese suggest that there is a distinct seasonal pattern of feeding correlated with the main growth periods of the different food plants.

4. Evidence is given which suggests that the diet of Brent geese may be much more restricted in Hampshire harbours than it is in Norfolk and Essex.

5. A feeding trial carried out on tame Pacific Brent (*Branta branta nigricans*) at the Wild-fowl Trust, Slimbridge, showed that analysis of the droppings gave a good approximation ($\pm$10 per cent.) of the proportions of food actually ingested.

6. Nutritional analyses of the main foods of Brent geese and of droppings derived from these foods are reported.

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REFERENCES

Burton, P. J. K. (1957). Private communication.

Butcher, R. W. (1941). The distribution of Zostera (Eelgrass, Wigeon Grass) and other seashore plants in relation to the migrations of wildfowl. *International Wildfowl Inquiry, Vol. I, Ch. III, p.* 29-49.

Campbell, J. W. (1946). The food of the Wigeon and Brent goose. *Brit. Birds*, **39**, 194-200 & 226-232.

Chapman, A. (1889). *Birdlife of the Borders*. London.

Cottam, C. (1935). The eelgrass shortage in relation to waterfowl. *Game Conf. Trans.*, **20**, 272-279.

Cottam, C., Lynch, J. F. & Nelson, A. L. (1944). Food Habits and management of American Sea Brant. *J. Wildlife Man.*, **18**, 449-460.

Ingram, C. (1933). Cattle feeding on geese droppings. *Brit. Birds*, **26**, 309-310.

Mörzer Bruijns, M. D. (1955). The Brent Goose (*Branta Bernicla*) on Terschelling (Netherlands). "*Ardea,*" *Tijdschrift der Nederlandse Ornithologische, Vereniging Jarrgang* 43, *aflevering*, **4**, 261-271.

Parish, E. L. (1953-54). The Brent Geese I-IV. *Shooting Times*, **71**, 395-396, 728-729, 816-817; **72**, 195-196, 208.

Steers, J. A. (1948). *The Coastline of England and Wales*. Cambridge University Press.

Storey, G. W. (1957). Private communication.

Sturkie, P. D. (1954). Passage of ingesta through avian tract. *Avian Physiology*. New York: Comstock.

Tugarinov, A. I. (1941). ("Anseriniformes") Faune de l'URSS, *publ. Acad. Sci. Aves*, **1** (4).

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1943). *The handbook of British Birds*, London: H. F. & G. Witherby. Vol. III, 210-215.

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OBSERVATIONS ON THE SEXUAL BEHAVIOUR OF INTERSEXES IN *Drosophila subobscura*

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Introduction

Sturtevant (1920) reported that intersexes in *Drosophila simulans* were courted by males, but themselves behaved indifferently towards other flies. Dobzhansky (1930) reported that some of the triploid intersexes in *Drosophila melanogaster* behaved like males, courting, mating and inseminating females. These intersexes were morphologically indistinguishable from males, but were sterile, producing non-motile sperm.

Apart from these cases, the sexual behaviour of insect intersexes is not known to have been studied previously to the present investigation.

The sexual behaviour of intersexes in *Drosophila subobscura* is of interest because it is more elaborate than the behaviour of the *D. melanogaster* intersexes in that they may show both male-like and female-like sexual behaviour.

Material

Intersexes in *Drosophila subobscura* are caused by a recessive autosomal mutation, *intersex*, which transforms XX individuals into male-like individuals. The intersexes were discovered by Dr. R. Milani of the Institute of Zoology, University of Pavia, among the offspring of a wild-caught female while he was working in the Zoology Department, University of Cambridge, in 1950.

A preliminary study of the intersexes has been made by Spurway & Haldane (1954). A more detailed account is in the course of preparation by the writer. It has been found that the intersexes can be arranged in a series from extremely female-like forms to extremely male-like forms. In this series there is a simultaneous reduction of the female internal and external genitalia and an increase in the male genitalia. The gonads range from ovaries indistinguishable from those of a female to intermediate undifferentiated gonads which have a pigmented sheath, such as is found on testes. The secondary sexual characters, such as the tarsal sex combs, are similarly intermediate in character in intersexes.

Normal Sexual Behaviour in *Drosophila subobscura*

Normal sexual behaviour in *Drosophila subobscura* has been described in detail by Rendel (1945), Milani (1951), Spieth (1952) and Maynard Smith (1956). Sexual behaviour in this species can be divided into the following stages:

(1). The reception of the visual stimulus by the male. (Mating will not occur in the dark in this species.).

(2) The approach and the flicking of the wings by the male. (Maynard Smith (1956) incorrectly uses the term scissoring to describe this wing movement.).

(3) The mutual tapping with the fore-legs, and the dance by the male and female.

(4) The posturing by the male and his acceptance by the female.

(5) Mounting, copulation and insemination.

Remating does not readily occur in *Drosophila subobscura*. Maynard Smith (1956) found that remating will occur if the first mating did not result in insemination or when an inseminated female has run out of sperm.

Female-like Behaviour

Eight very female-like intersexes were paired with males in 3″ x 1″ glass food vials. The pairs were put in darkness before either had recovered from etherisation. Mating occurred in six pairs in the first period of observation of approximately one hour. The eight pairs were then returned to the dark and left for three days, after which they were brought back into the light. Mating occurred in one of the unmated pairs, the intersex in the other pair having died. Remating occurred in three pairs, and was attempted in two others, the males in these cases failing to maintain their position on the intersexes. The seven pairs were returned to the dark for a few hours. Remating then occurred in a fourth pair. The pairs were returned to the dark for three days. A second remating was observed in one pair when the vials were brought back into the

light. This intersex had therefore been mated three times in six days.

In another series of observations about 100 intersexes were mated with males with the object of testing the fertility of intersexes. Of these only eleven laid eggs. The eggs laid by some of the intersexes were imperfect. They were of abnormal shape and had a thin and transparent instead of the normal thick and opaque chorion. One of the eleven intersexes laid 75 eggs in six days. All these were of normal appearance and were properly embedded in the food medium. Many of the eggs laid by the other intersexes were not embedded in the medium and were left on the surface. This is attributed to structural abnormalities in the genitalia rather than to abnormal behaviour. None of the eggs laid by the intersexes hatched. Female-like intersexes appear to be sterile.

Intersexes are remarkable in that they will readily remate. Unlike females, inseminated intersexes do not repel courting males. This could be either because they were unable to prevent the male from mounting, due to physical inability, that is, the effects of inbreeding and of the mutation, or because they were genetically abnormal, having genetically determined abnormal behaviour.

To test the possibility that intersexes were unable to prevent remating because they were physically unable to prevent the males from mounting, hybrid, and, therefore, vigorous males were mated to highly inbred females which were homozygous for a number of recessive mutations. These females were both physically disabled and lacking in vigour, more so than the intersexes.

Virgin females were collected from the *s th int ey wt*, *y ct cp sn v* and the *m ct cp sn v sc** stocks. Several attempts were made to induce remating. A second mating was attempted in eight cases out of 97, but no male was observed to mount and copulate. All the males courted vigorously.

It would appear that remating occurs in intersexes because intersexes lack that something which prevents a female from accepting a male once she has been inseminated. This difference is presumably genetical and a pleiotropism of the *intersex* gene.

**s*=scarlet (eyes)
th=thin (wings)
int=interrupted (venation)
ey=eyeless
wt=white testis
y=yellow (body)
ct=cut (wing margin)
cp=copper (eyes)
sn=singed (bristles)
v=vermilion (eyes)
m=miniature (wings)
sc=scute (missing scutellar bristles)

Male-like Behaviour

The first indication of male-like behaviour in intersexes was the occurrence of flicking in a vial containing a number of intersexes.

Male-like behaviour was studied by pairing intersexes with virgin females. The vials were kept in darkness between observations. It was immediately apparent that intersexes could be divided into two groups, those that invariably flicked and those that never flicked. The latter behaved indifferently towards the females, whereas the former showed male-like behaviour. 29 "flickers" and 79 "non-flickers" were observed in one series of observations on intersexes derived from one generation of the *intersex* stock.

All the "flickers" approached the female and flicked their wings, the flicking becoming more intense the closer they came to a female. Mutual tapping with the fore-legs was seen in most cases, but except in two pairs courtship did not proceed further. Posturing and dancing occurred in these. In one pair the intersex attempted to mount, but failed. This intersex was female-like in structure. It extruded its genitalia when posturing, an activity which could represent the flexing of the post-abdomen in posturing males,

The internal and external reproductive organs of "flickers" and "non-flickers" were examined, but the former were not found to be more male-like than the latter.

Discussion

Hollingsworth (1955) found that the sexual behaviour of a fore-and-aft gynandromorph in this species was determined by the genetic constitution of the anterior part, the region containing the brain. It would appear that the sexual behaviour of intersexes is likewise controlled by the brain. However, Milani & Rivosecchi (1954) reported that gynandromorphs in *Musca domestica* showed sexual behaviour corresponding to the sex of their abdomens. This observation is difficult to interpret in terms of the known physiology of insects, for it implies that some secretion of the reproductive system determines sexual behaviour in *Musca domestica*.

Summary

Intersexes in *Drosophila subobscura* may exhibit both female-like and male-like sexual

behaviour. The most female-like intersexes are mated by males and may lay eggs. None of these eggs has been known to hatch. Unlike females, intersexes permit remating by males. This is probably due to abnormal behaviour rather than to physical inability in preventing males from mating. Male-like behaviour is exhibited by only a few intersexes. This consists of the early stages of courtship, although one intersex was observed to attempt to mate, but failed.

REFERENCES

Dobzhansky, Th. (1930). Studies on intersexes and supersexes in *Drosophila melanogaster*. *Bull. Bur. Genet., Leningr.*, **8**, 91-158 (In Russian).

Hollingsworth, M. J. (1955). A gynandromorph segregating for autosomal mutants in *Drosophila subobscura*. *J. Genet.*, **53**, 131-135.

Maynard Smith, J. (1956). Fertility, mating behaviour and sexual selection in *Drosophila subobscura*. *J. Genet.*, **54**, 261-279.

Milani, R. (1951). Osservazioni sul corteggiamento de *Drosophila subobscura*. *Inst. Lombardo di Sci. e Lett.*, **84**, 1-12.

Milani, R. & Rivosecchi, L. (1954). Gynandromorphs and intersexuality in *M. domestica*. *Drosophila Information Service*, **28**, 135.

Rendel, J. M. (1945). The genetics and cytology of *Drosophila subobscura*. II. Normal and selective matings in *Drosophila subobscura*. *J. Genet.*, **46**, 287-302.

Spieth, H. T. (1952). Mating behaviour in the genus *Drosophila*. *Bull. Amer. Mus. nat. Hist.*, **99**, 395-474.

Spurway, H. & Haldane, J. B. S. (1954). Genetics and cytology of *Drosophila subobscura*. IX. An autosomal recessive mutation transforming homogametic zygotes into intersexes. *J. Genet.*, **52**, 208-225.

Sturtevant, A. H. (1920). Intersexes in *Drosophila simulans*. *Science*, **51**, 352-353.

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THE SEXUAL ISOLATION BETWEEN *Drosophila melanogaster* AND *Drosophila simulans*

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Introduction

Behavioural barriers to inter-specific hybridization are widespread in Drosophila, and their effects have been measured in a number of ways for a wide range of species, (see Patterson & Stone, 1952, for a thorough review of the literature to that date). It is usual for females of one species to recognise and discriminate against all foreign males, though such discrimination may not be absolute, and often the males also discriminate and do not court foreign females so frequently as their own. In relatively few cases, however, have the stimuli involved in specific recognition been analysed. Mayr (1950) showed that removing the antennae from females of *D. pseudoobscura* and *persimilis* almost completely prevented them discriminating between males of their own and the other species. Similarly, Spieth (1952) showed that removing the fore-tarsi from males of two strains of *D. virilis* hampered their discrimination of their own females from related ones, which they must normally recognise by contact chemical stimuli when they tap with the fore-legs prior to courtship. The tarsi of many Diptera have long been known to be richly provided with chemosensory hairs.

This paper describes some experiments which analyse to a certain extent the basis for the strong sexual isolation between the very closely related *D. melanogaster* and *D. simulans*. The hybridization of these species was first described by Sturtevant (1920) who found, as have many workers since, that the cross using *melanogaster* males and *simulans* females is more difficult than the converse one. Drosophila workers generally recommend that for either cross aged males should be used with very young females to obtain the greatest success, although the reasons for this are not clear.

Various genetical stocks of closely related species will almost certainly differ in their degree of isolation. Koopman's (1950) work with *pseudoobscura* and *persimilis*, for example, shows how easily selection can alter isolation, so the quantitative data provided here are only valid for the stocks used. The qualitative stimuli involved in isolation probably vary rather less and one is safer in making generalizations.

Materials and Methods

The stocks used were all "wild-type" and kept as outbred as possible. A large number of pairs were used to found each generation and new stocks, including some caught in the wild, were added as they were obtained, though not during the course of these experiments. For single pair matings and observation of courtship small perspex cells were used (see Bastock & Manning, 1955) whilst mass matings were made in 3″ × 1″ vials with food. The flies were reared and the experiments all made at 25°C.

The Receptiveness of Females

As mentioned above, females are said to be more receptive to foreign males when they are young, and Table I shows the results of one experiment to test this. Five 3-day-old males of one species and ten 1- or 3-day-old females of the other were put unetherised into a vial with food, and the females dissected at the end of 48 hours to determine the number inseminated. No females which were 3 days old at the start of the experiment had been inseminated, but a small percentage of those that were only 1 day old at the start were fertilized, and *melanogaster* females

Table I. The Proportion of Females Inseminated by Foreign Males in 48 Hours. Five ♂♂ and 10♀♀ in a 3″ × 1″ vial with food—a few females were lost during transfers and dissection. Female age refers to that at start of test; all males were 3 days old at start.

	1-day ♀♀	3-day ♀♀	Antennaless 1-day ♀♀
Sim. ♂♂ × mel. ♀♀	35/147	0/136	15/146
Mel. ♂♂ × sim. ♀♀	10/140	0/137	9/134

had accepted about three times as many foreign males as had *simulans*.

It is of interest to see if this apparent fall in receptivity with age is true of females courted by their own males, and to this end, a large number of single pair matings were timed using females of various ages, but always with mature 3-day-old males. Both males and females were transferred to fresh food every day and not more than twenty insects were kept in a vial together whilst ageing. Under such conditions almost 100 per cent. of males court well within a few seconds of introduction with a female into an observation cell. Only courtships which were practically continuous were recorded and males were discarded unless they began to court within 2 minutes. At the end of 20 minutes continuous courtship without copulation the pair was discarded and a courtship time of "20+ minutes" recorded. Fig. 1. shows histograms of the courtship time to copulation, grouped in 2-minute intervals, with females of different ages. It is not possible to detect any differences in the courtship of males with females of the different ages, and thus the variation due to individual male differences is probably equal for each histogram. With both species it is clear that females are most receptive, and least variable in this respect, when 3 days from eclosion and that there is a gradual increase in receptiveness with ageing up to 3 days. By 4 days from eclosion there are some signs of increased variability and decreased receptiveness, but measures of virgins 10 days old or more (not illustrated) show very little change from the 4-day averages. Receptiveness probably declines slowly after the slight falling off from the peak at 3 days old. Very old virgins —some were tested at an age of 85 days—are very unreceptive and extrude their ovipositor when courted in the manner of fertilized females.

It seems very likely that this receptivity peak is correlated with the maturation of the ovaries which also reach a maximum at about this age. The effect of ovarial growth is unlikely to be a direct one; no kind of sex hormone has been demonstrated in insects and Maynard Smith (1958), who finds the same increase in receptiveness in *D. subobscura*, has shown that congenitally ovariless females go through the same behavioural cycle as normal ones.

Since the receptivity of females towards their own males is lowest when they are newly emerged it is unlikely that the increased success of foreign males with young females can be explained in terms of higher receptivity. It is necessary therefore to consider either that young females cannot discriminate so well as older ones, or that males do not court the different age groups of foreign females equally. We may now consider evidence which bears on the second of these possibilities.

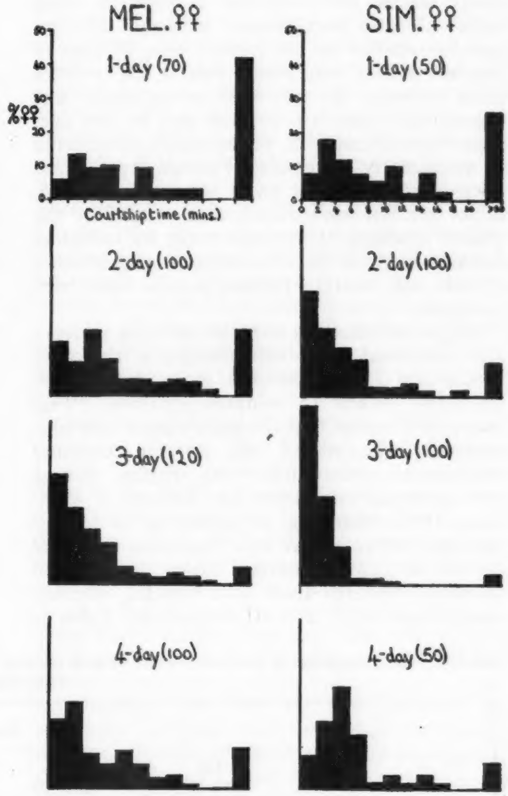

Fig. 1. The receptivity of females with agd, expressed as the percentage copulating within a given time with 3-day-old males. Each block of the histograms represents a span of 2 minutes and its height denotes the percentage of females which accepted males after the corresponding period of continuous courtship. The bracketed figures after the age of the females give the number of pairs recorded for each histogram.

Discrimination by Males

Males of both *melanogaster* and *simulans* from a few hours of age will approach most moving objects of roughly the right size and tap with their fore-tarsi. They will court their own females when these are any age from a few hours to

many weeks, and will also attempt to court males of their own species, although they are rapidly repelled by the violent wing-flicking of courted males. Very young flies, a few minutes from eclosion, do not seem so attractive but occasionally they are courted and at this age, since they cannot flick, young males are courted as persistently as females. Foreign females are also courted in some cases for, once aroused, males are not immediately discouraged by the milder repelling movements made by unwilling females. Some of the factors determining whether a male will court a foreign female have been analysed.

Single pair matings were set up using in every case 3-day-old males with females of the other species and the proportion of males showing full courtship within 15 minutes recorded. "Full courtship" means that the male tapped and subsequently showed all the normal courtship movements, orientation, wing display, licking and attempted copulation (see Bastock & Manning, 1955; Manning, in press) for at least 2 minutes. We may take as a "base-line" a figure of 100 per cent. of normal males showing full courtship towards their own females, whether these latter are 1, 2, 3 or 4 days old. Table II (top line for each species) shows the proportion of normal males courting foreign females of different ages. It can be seen that almost all *melanogaster* males court 1- and 2-day-old *simulans* females, but that only half of them will court 3-day-old females and when the *simulans* females are 4 days old only 8 per cent. are courted. It appears then, that between 2 and 3 days of age some change occurs to *simulans* females which causes *melanogaster* males to discriminate against them; they are approached and tapped, but then the males turn away without further courtship. A similar pattern is found with *simulans* males and *melanogaster* females. Here though, far fewer females are courted, about 25 per cent. when they are only 1 day old, but if they are any older than this the males always reject them after tapping. It may be that the change with age corresponding to that in *simulans* females occurs between 1 and 2 days of age with *melanogaster* females.

Since the rejection of foreign females always follows tapping it was obviously necessary to test the responses of males whose fore-tarsi had been removed. Spieth (1952) showed that this operation increased the number of foreign females inseminated by males of one *D. virilis* strain, but

Table II. The Proportion of 3-day-old Males of both Species Showing full Courtship to their Own and Foreign Females of Different Ages.

	Melanogaster ♂♂ with:—				
	3 day mel. ♀♀	1 day sim. ♀♀	2 day sim. ♀♀	3 day sim. ♀♀	4 day sim. ♀♀
Normal ♂♂	(100%)	29/35 83%	26/30 87%	18/40 45%	4/50 8%
Tarsi-less ♂♂	36/40 90%	26/30 87%		24/40 60%	23/40 57%
Antennaless ♂♂	39/40 97%	26/30 87%		24/40 60%	10/40 25%
	Simulans ♂♂ with:				
	3 day sim. ♀♀	1 day mel. ♀♀	2 day mel. ♀♀	3 day mel. ♀♀	
Normal ♂♂	(100%)	10/40 25%	0/30 0%	0/40 0%	
Tarsi-less ♂♂	29/40 72%	18/40 45%		16/50 32%	
Antennaless ♂♂	29/40 72%	5/40 12%	0/20 0%	0/40 0%	

he did not observe the effect upon the males' behaviour. As shown on Table II, *melanogaster* males without their fore-tarsi court their own females practically normally, only four out of forty failing to respond. *Simulans* males do show a significant reduction ($x^2=10{\cdot}55$, $P<0{\cdot}01$) following the operation, but nearly three-quarters of them court. Tarsi-less males approach and try to tap the females, usually coming closer to them than normal and pushing part of the way on to the female's back with the stumps of their fore-legs. Most of the operated males are sufficiently aroused for their subsequent courtship is quite normal, although they lag behind the females somewhat because their running is hampered. It appears that the chemical stimuli received by a male on tapping are not essential for arousal in most cases.

The results with foreign females show conclusively that tarsi-less males do not distinguish foreign females so well as intact ones. With *melanogaster* the proportion of tarsi-less males courting 3-day-old *simulans* females is somewhat increased over normal, and that courting 4-day-old females is very greatly increased by some seven times ($x^2=23{\cdot}62$, $P<0{\cdot}001$). This pattern is even more vivid with operated *simulans* males. Here the proportion courting 1-day-old *melanogaster* females is nearly doubled and nearly one third of tarsi-less males show full courtship to 3-day-old females which are never courted by normal males. Thus although no essential positive stimuli results from tapping conspecific females, it appears that inhibitory stimuli normally result from tapping mature foreign females. In the absence of these inhibitory stimuli, the other positive stimuli to courtship which such females provide suffice to elicit a response in many cases.

A further series of tests was performed with males whose antennae had been removed. Mayr (1946) found that this operation slightly reduced the isolation between *pseudoobscura* and *persimilis*. Begg & Packman (1951) who used *melanogaster* with varying manifestations of the gene "antennaless", found that flies without antennae produced very few inseminated females when crossed and there were clear indications of reduced sexual activity from males as well as females. It seems possible that this may be due to other side effects of the antennaless gene, for I find very little sign of reduction in sexual activity with normal *melanogaster* males whose antennae are removed. All but one of the forty antennaless males showed full and vigorous courtship towards their own females and they copulated within the normal time range. There was some indication that they took a little longer before they approached and tapped females, but lowered general activity is typical of flies without their antennae and is not specific to sexual behaviour. As with removing the tarsi, so the operation of removing antennae did reduce the number of *simulans* males which were aroused ($x^2=10{\cdot}55$, $P<0{\cdot}01$) and some 25 per cent. did not court their own females. Antennaless *simulans* are very sluggish indeed, but most that did approach and tap females were aroused and copulated in normal times.

Loss of the antennae had rather different effects on isolation with the two species. With *melanogaster* the proportion of antennaless males that court 1- or 3-day-old *simulans* females is no different from normal. More court 4-day-old females than normal (the difference is just significant at the 5 per cent. level on these figures, $x^2=3{\cdot}81$) but a smaller proportion than was the case with tarsi-less males (x^2 for the difference$=7{\cdot}42$, $P<0{\cdot}01$). However with *simulans* the antennaless males are more isolated than normal flies, for only five out of forty such males court 1-day-old *melanogaster* females and none court females older than this. This may simply be due to the raised reaction thresholds of antennaless *simulans* males, but it is also possible that stimuli perceived by the antennae are relatively less important for the discrimination of foreign females in *simulans* than *melanogaster*. Consequently inhibitory stimuli received by the tarsi are able to prevent courtship even though any inhibition via the antennae has been eliminated, while in *melanogaster* the absence of antennal inhibitory stimuli decreases discrimination even in the presence of the tarsi. Even if the two species do differ in this respect, there is little doubt that the fore-tarsi are absolutely more important for discrimination in *melanogaster* too for, as we have seen, their removal produces a greater reduction in isolation than loss of the antennae.

Summarising, we may conclude that males of both species court young foreign females better than old ones and that the increasing discrimination against the latter as they age is related to the strengthening of some species-specific scent. The evidence gained from depriving males of various sense organs indicates that this specific scent is concentrated on the female's body surface, but some is probably air-borne and can be detected by a male without fore-tarsi when he is

close to the female. Neither tarsal chemoreceptors or the scent receptors of the antennae are necessary to arouse courtship, and about 50 per cent. of males from which both have been removed still court their own females fairly well. However both sets of receptors, and especially those of the fore-tarsi, are sources of inhibiting inputs when a male approaches and taps a mature foreign female.

It would be of great interest to see whether the particular chemoreceptor neurones which respond to a foreign female's scent correspond to those described by Dethier (1955) in *Phormia* which react to unpleasant substances. *Phormia* chemoreceptors have another neurone which responds only to sugars and other pleasant substances, but the present experiments do not enable one to conclude with certainty that females of his own species provide a Drosophila male's chemoreceptors with a corresponding sexual stimulating substance. If so such stimulation is not indispensable for arousing him.

It is reasonable to conclude that the isolation between mature males and females of *melanogaster* and *simulans* is as much due to discrimination by the males as that of the females, but that between males and young foreign females is largely due to the females. In the former case any discrimination by the females is masked, since males do not try to court them. In fact mature females do discriminate strongly, for so far it has not been possible to get any inseminated 3-day-old females by putting them with tarsi-less males though these certainly court them better.

Discrimination by Females

We may now consider briefly the stimuli by which females recognise foreign males; so far all the evidence is of a negative kind. As was pointed out by Spieth (1952), neither visual stimuli nor a "sampling" of the courtship movements are likely to be involved. Foreign males are usually rejected from the instant they tap the female and have no more success in the dark than the light. Unlike Mayr's (1950) case with *pseudoobscura* and *persimilis*, removing the antennae from females does not affect their ability to discriminate. The third column of Table I shows the number of antennaless females, 1-day-old at the start of the experiment, which were fertilised by foreign males. The proportion is unchanged for *simulans* females, but even shows some reduction with *melanogaster*, which is probably correlated with the greater reduction in receptiveness which follows the loss of the antennae in this species compared with *simulans* (Manning, in press). Since the antennae are the chief receptors for air-borne chemical stimuli, one is left with the conclusion, already suggested by Spieth (1952) for some species, that it is largely by contact chemoreceptors that these females distinguish their own from foreign males. It is most likely that the male's act of tapping provides the female with chemical stimuli and thus a means of discriminating. It must be noted that foreign males lacking their fore-tarsi are rejected just as normal, so that probably any contact with the male's body is sufficient.

These results do not explain why more *simulans* males are eventually successful with foreign females for, in general, they court them less well than *melanogaster* males. Presumably *melanogaster* females are not so persistent in their discrimination and resist foreign courtship less.

The Behaviour of Hybrids

The hybrids between *melanogaster* and *simulans* might be expected to be roughly intermediate in their behaviour, but the small amount of information so far available does not confirm this. Sturtevant (1920) says that hybrid males will court either parent or hybrid females but gives no data on preferences. I have always found that the responses of male hybrids are scarcely separable from those of *simulans*. The courtship pattern is very similar, and combining several experiments, while 28/30 hybrid males courted 3-day-old *simulans* females, none (0/20) courted *melanogaster* females of the same age, though 2/10 courted 1-day-old females. A further 1/10 hybrid males courted 3-day-old hybrid females. Certainly the hybrid males seem to prefer *simulans* females and these were the only ones ever to accept them; copulation occurred after quite normal courtship times. Hybrid females, on the other hand, are only courted well by *melanogaster* males and I have not seen *simulans* males go beyond tapping them. This result may simply be due to the lower sexual response threshold in *melanogaster* and need not mean that the hybrid females produce a *melanogaster* type scent.

Discussion

We may deduce that the sexual isolation between *melanogaster* and *simulans* depends mostly upon female discrimination when the females are young, but by 3 days of age both sexes are discriminating, and by chemical rather than be-

havioural means. The specific scents involved appear to be relatively independent of environment in their development and recognition, for all attempts to influence isolation by rearing the two species together, both as larvae and adult, have so far failed. Mayr & Dobzhansky (1945) did succeed in influencing the isolation between *pseudoobscura* and *persimilis* by rearing them in mixed cultures. They found slightly increased isolation between flies exposed to the other species during development, but such an effect would be more difficult to demonstrate with *melanogaster* and *simulans* as their normal isolation is so much greater than that of the other sibling pair.

It is clearly advantageous tò have specific recognition based upon a clear-cut chemical difference. Such differences may be expected to arise at a relatively early stage in divergence from a common ancestor and provide a rapid means for recognising a suitable mate. It is not so clear why the specific scents of the females should take one or two days to become fully effective; rather little is known about the development of cuticular scent in Drosophila.

As a result of this slow development of scent, males may "waste" some of their attentions upon unsuitable mates. However in a mixed population under natural conditions, it is very unlikely that males will court young foreign females for long. Such females are giving more wing-flicking and other repelling stimuli and the courting males will soon desist and approach other females. Obviously it is advantageous for males, who will mate many times in succession, to be easily aroused and approach any fly in the vicinity to test its suitability. Females which probably rarely mate more than twice and are unreceptive to males for several days following copulation, must choose their mates with certainty.

Summary

1. Some of the stimuli involved in the sexual isolation between *D. melanogaster* and *D. simulans* have been analysed.

2. Females of both species show a slow rise in receptiveness to their own males which reaches a peak at 3 days of age and thereafter falls slowly. Foreign males are more successful with young (1-day-old) females than mature ones.

3. Males court young foreign females better than mature ones, but removing their fore-tarsi prevents their discriminating against the latter to a marked extent.

4. Antennaless *melanogaster* males also show some reduction in isolation, but this is not seen with *simulans*, whose males are more affected by sensory deprivation.

5. The behaviour of hybrid flies is briefly discussed.

REFERENCES

Bastock, M. & Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behaviour*, **8**, 85-111.

Begg, M. & Packmann, E. (1951). Antennae and mating behaviour in *Drosophila melanogaster*. *Nature*, (*Lond.*), **168**, 953.

Dethier, V. G. (1955). The physiology and histology of the contact chemoreceptors of the blowfly. *Quart. Rev. Biol.*, **30**, 348-371.

Koopman, K. F. (1950). Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Evolution*, **4**, 135-148.

Manning, A. (In press). The sexual behaviour of two sibling *Drosophila* species. *Behaviour*.

Maynard Smith, J. (1958). The effects of temperature and of egg-laying on the longevity of *Drosophila subobscura*. *J. exp. Biol.*, **35**, 832-842.

Mayr, E. (1946). Experiments on sexual isolation in Drosophila. VII. The nature of the isolating mechanisms between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Proc. nat. Acad. Sci.* (*Wash.*), **32**, 128-137.

Mayr, E. (1950). The role of the antennae in the mating behaviour of female Drosophila. *Evolution*, **4**, 149-154.

Mayr, E. & Dobzhansky, T. (1945). Experiments on sexual isolation in Drosophila. IV. Modification of the degree of isolation between *D. pseudoobscura* and *D. persimilis* and sexual preference in *D. prosaltans*. *Proc. nat. Acad. Sci.* (*Wash.*), **31**, 75-82.

Patterson, J. T. & Stone, W. S. (1952). *Evolution in the genus Drosophila*. New York: Macmillan.

Spieth, H. T. (1952). Mating behaviour within the genus *Drosophila* (*Diptera*). *Bull. amer. Mus. nat. Hist.*, **99**, 395-474.

Sturtevant, A. H. (1920). Genetic studies on *Drosophila simulans*. I. Introduction. Hybrids with *Drosophila melanogaster*. *Genetics*, **5**, 488-500.

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THE OCCURRENCE AND POSSIBLE SIGNIFICANCE OF THE "SHAKING" OF HONEYBEE QUEENS BY THE WORKERS

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Introduction

Up to the present only a very few reports have been published of the phenomenon of "shaking" in colonies of honeybees (*Apis mellifera* L.), in spite of the fact that it is a quite frequent occurrence. The process is very characteristic and at any one time is carried out by a relatively small number of workers in the colony. Each of these workers (which will be referred to as "shakers") moves in an apparently methodical way over the combs, from time to time grasping a bee with its fore-legs and then rapidly vibrating its body in a vertical plane for approximately one second. Alternatively, on some occasions the shaker may hold the other bees with all three pairs of legs or it may simply rest its head against their bodies while shaking. Therefore, although the act of shaking consists of a relatively stereotyped series of movements the grip of the shaker is variable.

Istomina-Tsvetkova (1953) and Schick (1953) have given descriptions of worker bees being shaken; Taranov & Ivanova (1946) also reported shaking but only in connection with the queen of a colony preparing to swarm, while Hammann (1957) described the shaking of newly-emerged queens but stated that she had never seen an established queen shaken, although she commented on the fact that foraging bees may shake neighbouring workers. A report of shaking of both queens and workers has also been given by Milum (1955). These rather diverse results have, however, yielded no clear information about the overall significance of shaking in the colony. The present paper, of which a preliminary report has already been published (Allen, 1958a), is a study of the problem in relation to the queen.

Methods

Observations were made on two colonies housed in observation hives which contained three or four British Standard brood combs and which allowed the bees free flight. In 1957 the observation hive of Colony C was equipped with a heating unit controlled at a nominal 27°C. at the thermostat. The number of bees in each colony was approximately as follows:

Colony B. 7th July, 1955: 9,500 bees.
Colony C. April and May, 1957: 4,000 bees.
18th June, 1957: 7,000 bees.
8th July, 1957: 10,500 bees.

Fifteen of the daily observation periods in 1955 had a duration of one hour, and four of half-an-hour, while on the day of swarming (7th July) there was one observation of five minutes. In 1957 the majority of the observations on the 72 different days considered had a duration of one hour (11 periods were less than one hour but not less than half-an-hour, and 8 periods exceeded one hour; full details are given by Allen, 1958b, Table XI).

In order to have bees of known age in the observation colonies groups of newly-emerged bees were taken from other colonies, were marked on the thorax with a spot of coloured cellulose paint, and were then allowed to dry for about 30 minutes before being introduced into the observation hive. Introductions were carried out as follows:

1955: groups of 200 bees introduced twice weekly from 26th April to 5th July.
1957: groups of 100-110 bees introduced twice weekly from 28th March to 9th July.

Results

(1) Frequency of Shaking

Preliminary observations were made on Colony B between 9th May and 7th July, 1955, and detailed daily observations on Colony C between 11th April and 13th July, 1957. In both cases the final date was that on which the swarm departed, but in August and September, 1957, additional records were made of the shaking of the newly-mated queen in Colony C.

The queen of Colony B was not seen to be shaken until after swarm preparations (in the form of queen cup building) had commenced. In this colony there was a long interval between the appearance of the first and the second queen cups and the rapid formation of queen cups began only on about 24th June. Coinciding with this period of active swarm preparations, the

queen was shaken progressively more frequently, as shown in Fig. 1. The swarm left the hive on 7th July, but the queen failed to join the departing bees and in consequence they returned to the

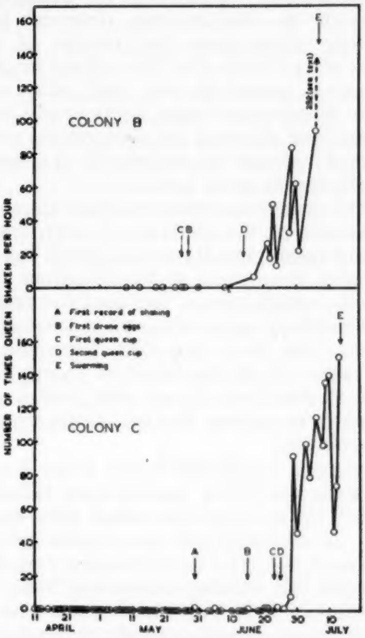

Fig. 1. Frequency with which queens were shaken.

hive after approximately half an hour. During this time the queen was surrounded by agitated bees, and after a further 30 minutes had elapsed a five-minute count of the number shaking her was made. The frequency proved to be the highest recorded in the present observations, for 21 bees shook her in this period (252 per hour).

In Colony C the formation of the first queen cup marked the start of the rapid building of queen cells, and here also swarm preparations were accompanied by a sudden increase in shaking from a minimal level to a peak at the time of swarming (Fig. 1).

Both graphs shown in Fig. 1 thus demonstrate very clearly that before swarm preparations had commenced the queen was shaken only very occasionally, and that in the two or three weeks preceding the issue of the swarm there was a sudden increase in frequency so that she was shaken once or twice per minute. This very pronounced rise in both colonies during the same period of development strongly suggests a connection with swarming, and this hypothesis is supported by the fact that the initial increase in shaking followed very quickly upon the start of rapid queen cup formation.

It seemed relevant to consider whether the lack of shaking of the queen in the period prior to swarm preparations was due to the absence of shakers in her neighbourhood. Since it had been found that, in contrast to the queen, the workers might be shaken at any time of the year (Allen, 1958b), the problem was solved by observing if any marked shaker of the workers came near the queen but did not shake her. In Colony C the results were that 43 such shakers were observed to join the queen's circle of attendants and examine her with their antennae but subsequently were seen to depart without shaking her. The details are given in Fig. 2. Comparing this distribution with that of the frequency of shaking of

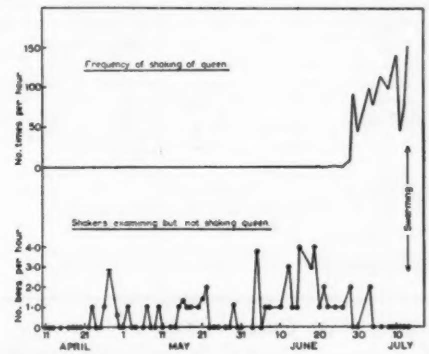

Fig. 2. Incidence of shakers examining but failing to shake the queen.

the queen of the same colony (taken from Fig. 1) it is immediately apparent that many shakers had the opportunity to shake the queen before swarm preparations began but failed to do so. In this connection it is interesting to note that Hammann (1957) also observed that bees shaking the workers apparently did not shake the newly-emerged queen.

After the queen of Colony C had departed with the swarm on 13th July the author destroyed all the remaining queen cells except one. The young queen from this cell emerged on 19th July but unfortunately it was not possible to make further detailed observations until 2nd August, the date on which she commenced laying, presumably after making mating flights on one or more of the previous three fine days.

To determine whether the queen was shaken at this stage of her life further observations were carried out on seven different days between 2nd August and 3rd September over periods having a mean duration of 18 minutes. The results are given in Table I and they show that a newly-mated queen may be shaken for a few days after she has begun to lay, but there is every indication that shaking is continued for a short period only and that once she is well established in the colony the shaking ceases.

Table I. Frequency with which Newly-mated Queen of Colony C was Shaken.

Date	No. of times queen shaken per hour	Notes
2nd August	27	First day of laying
3rd August	9	
7th August	6	3 rebuilt queen cups receiving considerable attention from bees.
12th August	0	Queen cups receiving less attention.
16th August	0	
31st August	0	
3rd September	0	

(2) Ages of the Queen's Shakers

In Colonies B and C the ages of all marked shakers of the queen were recorded up to the time when the swarms left, and the total numbers of each age are given in Fig. 3. Their age range was 3 to 61 days, but the greatest numbers occurred in approximately the fourth week of adult life. The total number of marked bees in the colony inevitably fell progressively with age (since there is a greater likelihood of death with increasing age), and taking this into consideration the shape of the curve in Fig. 3 indicates that only a very low proportion of young bees shook the queen, but that the proportion rose with the age of the shakers, at least up to about 30 days.

Discussion

Observations made by Milum (1955) on shaking, which he calls "spirit tapping" or "D-VAV" (dorso-ventral abdominal vibration), support the view that the shaking of the queen is connected with swarm preparations, since he reports that during four years he saw both mated queens and virgins shaken before they left with swarms, although he mentions one mated queen on which no shaking was observed before swarming. Apart from two records of caged queens being shaken after their release he saw no shaking of queens at any time except when swarm preparations were being made in the colonies, and although his observations are not described in detail they are broadly in agreement with the results given here.

In the present colonies no observations were carried out on the shaking of newly-emerged unmated queens but Hammann (1957) has given a detailed description of the behaviour of the workers to such queens. She used five colonies, which had their queens removed on various dates between 23rd May and 20th September, for observation of the treatment of young queens reared in emergency queen cells, and it seems reasonable to suppose that her results are generally applicable.

Hammann found that within a few hours of emergence the young queens were licked and touched by the workers, which also made a series of characteristic movements in their neighbourhood. The most frequently occurring movement was shaking, comprising 56 per cent. of a total of 1850 single movements observed. The frequency of shaking on the queen or in her neighbourhood was 1,200 times per hour when measured over a period of one hour at noon on a warm June day, but was reduced in the morning and evening and on cold days. The so-called "attacks" on the queen, consisting of "shaking," "bumping," "rocking" and other movements,

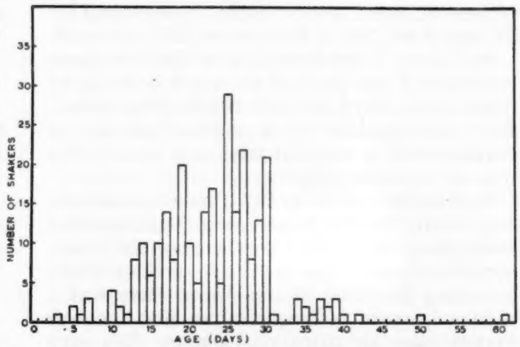

Fig. 3. Ages of workers shaking the queens in Colonies B and C.

appeared to result in greatly increasing her activity until she eventually left the hive on a mating flight. After each flight the attacks subsided for a time only to increase again before the next flight. Following the final mating flight shaking and the other movements were still to be observed but gradually became gentler and less frequent, and ceased altogether if the queen started laying.

When Hammann's results on unmated queens are taken in conjunction with those obtained here for mated queens in Colonies B and C it seems almost certain that the shaking of the queen is a mechanism in some way preparing her for flight, for it is surely not by chance that the only times when she is shaken are before swarming and in the mating period. It may also be assumed that the incidence of the shaking of the queen is governed at least partly by an internal (colony) factor since it occurs at definite stages in colony development and ceases soon after eggs are laid, but not immediately after the act of mating. It may, in addition, be influenced by external factors such as weather conditions.

Summary

1. The phenomenon of "shaking" in honeybee colonies is described, and is here considered in relation to the queen of the colony.

2. The queen was rarely shaken in the spring but once swarm preparations had commenced the frequency of shaking rose rapidly, reaching a peak at about the time the swarm left. A newly-mated young queen was shaken to some extent just after she first commenced laying, but within a few days the frequency had fallen markedly, and finally no shaking was observed. Since the queens were shaken only at times when they were likely to fly out of the hive it is concluded that there is a connection between the two events. Hammann (1957) gives results on unmated queens which also support this assumption, for these queens were shaken with increasing frequency before each mating flight.

3. The ages of the queen's shakers ranged from 3 to 61 days but the greatest numbers occurred in approximately the fourth week of adult life.

REFERENCES

Allen, M. Delia (1958a). The shaking of honeybee queens prior to flight. *Nature* (*Lond.*), **181**, 68.

Allen, M. Delia (1958b). A study of some activities of the honeybee. *Univ. of London: Ph.D. Thesis.*

Hammann, Eleanore (1957). Wer hat die Initiativ bei den Ausflügen der Jungkönigin, die Königin oder der Arbeitsbienen? *Insectes sociaux*, **4**, 91-105.

Istomina-Tsvetkova, K. P. (1953). (New data on the behaviour of bees). *Pchelovodsyvo* (9), 15-23.

Milum, V. G. (1955). Honey bee communication. *Amer. Bee J.*, **95**, 97-104.

Schick, W. (1953). Über die Wirkung von Giftstoffen auf die Tänze der Bienen. *Z. vergl. Physiol.*, **35**, 105-128.

Taranov, G. F. & Ivanova, L. V. (1946). (Observations on the behaviour of the queen in the colony). *Pchelovodstvo*, (2/3), 35-39.

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GROUP FORMATION IN THE THYSANURA

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Allee (1931) recognised the existence of two major types of animal aggregations: "associations", primarily the resultant of the reactions of individuals to environmental stimuli, and "societies", of individuals to one another. He, like Deegener (1918) before him, claimed that societies can be founded and maintained in response to asexual as well as sexual stimuli. The degree of sociality is conditioned by the closeness of integration, stability and permanence of the group.

The results now presented indicate that the Thysanuran *Petrobius brevistylis* Carpenter has a weakly developed sociality founded on an asexual basis.

Field Observations

Petrobius brevistylis is a primitively wingless insect, one inch long when adult, found in considerable numbers around the coastlines of the British Isles. Its natural habitat is among stones, boulders and outcrops of the parent rock on the sea shore immediately above high-water mark. In collecting these insects at various times of the year a number of features of their behaviour were noted. Collections were only made during daylight, when it was uncommon (with the exception cited below) to find any outside secluded haunts. They were generally found in local aggregations on the undersurfaces of rocks and stones and within crevices of the parent rock and larger boulders. The groups were motionless until disturbed. The few *Petrobius* which were seen running over the rocks were isolated individuals. These observations confirmed those of Wygodzinsky (1941) who noted that Machilids usually move and feed at night and by day they become relatively inactive; Lie-Pettersen (1907) briefly reported on the existence of groups in *Machilis* (probably *Petrobius*) *maritimus*.

The size of groups and their location appeared to vary with the age of their members. The eggs of *Petrobius* hatch in May, and by mid-June the young insects have a body length of approximateately 5 mm. At this stage they were seen in clusters of several hundred individuals, on exposed rock surfaces. This behaviour was only observed during June and July. At other times of the year the groups were smaller—from three to sixty—and found only in secluded situations. There was generally a very short pause, on raising a stone, before the group displayed any activity. All the individuals then appeared to move simultaneously; some jumped and the remainder ran rapidly.

In addition to the groups, solitary individuals were common. The position of one member of a group with respect to another did not display any distinct pattern. Each group tended to be in a compact circular or sub-circular cluster, and the insects usually rested with their very long antennae overlying another member of the aggregation. Insects were absent from areas adjoining those populated by groups although physical conditions were apparently similar, and so it was concluded that the insects arranged themselves into groups caused at least in part by mutual attraction. Laboratory experiments were designed to test this conclusion and to discover the origin of the groups, their method of maintenance and the extent of their social organisation.

The insects were observed at, and collected from, an area of broken and eroded sandstone cliffs near Sidmouth, Devonshire.

Preliminary Experiments

These were to determine whether a set of physical conditions could be provided to which the insects would show a positive response. Also, if such conditions were duplicated, whether insects would disperse randomly. It was hoped to estimate the strength of any mutual attraction, as distinct from purely physical responses that might operate.

The experiments were conducted in a glass tank (24″ × 11″ × 11″ high) with metal supports along its outer edges. The floor of the tank was covered with white paper, which provided a surface over which the insects could move easily and be clearly seen.The paper was held in position by transparent adhesive tape, 0·6″ wide, half its width attached to the perimeter of the paper and the other half to the side walls of the tank; the highly glazed tape offered a surface on which the insects had difficulty keeping a

foothold. This eliminated the tendency of *Petrobius* to move into contact with the side walls and corners of the tank. Five 3″ × 3″ squares of Bristol Board, supported at each of their corners by a small block of plasticine 0·25″ thick, were arranged as shown in Fig. 1. A 40-watt pearl electric lamp bulb, placed directly over Card 3

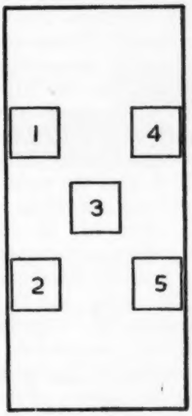


Fig. 1. Plan of glass tank used in Experiments 1-7. The squares 1-5 are the positions of the cards.

and 15″ above the base of the tank, provided the only source of illumination. The experiments took place in a dark room during February, 1953, at temperatures of 12·5 to 14°C. Fifty-six recently captured *Petrobius* were released into the tank, randomly dispersed by waving a hand a few inches above them, and observed for 30 or 50 minutes. Throughout this time they displayed considerable activity, visiting all parts of the tank available to them, including the upper surfaces of the cards. Though they might go beneath a particular card, they would not necessarily stay there but frequently passed from one card to another. Groups only formed beneath cards. To determine the numerical arrangement of the individuals at the termination of each experimental period the following procedure was adopted. The number of insects not under any card was counted first. The cards under which fewest insects had been observed to go were lifted, and the number beneath them counted. The number under the fifth and last card was obtained by subtracting the total already counted from the total used in the experiment. This method obviated having to make a rapid count of a large number of individuals.

The results of the seven experiments are given in Table I. At the end, 306 out of 392 bristle-tails were beneath cards. Card 3 was visited least, having only 11 insects beneath it in the seven experiments. Cards 4 and 5 were also seldom visited. Experiments 6 and 7 attempted to determine whether some unobserved physical factor was responsible for the way the insects organised themselves beneath Card 1. Only in Experiment 7 had this been partly achieved. Had the animals aggregated under Card 1 in response to some unmeasured peculiarity with respect to height of the card above the substrate, then the decline in numbers from beneath this card could be expected to be compensated by an increase under Card 5. This did not, in fact, take place.

Table I. Dispersion of *Petrobius brevistylis* Carp. beneath Cards (Experiments 1-7).

Experiment	1	2	3	4	5	6	7
Experimental conditions	As in Fig. 1			As in Fig. 1 except whole tank rotated through 180°		As in Fig. 1 except cards 1 and 3 interchanged	As in Fig. 1 except plasticine bases 1 and 5 interchanged
Duration (min.)	30	30	30	50	50	30	30
No. of insects under:							
Card 1	32	42	38	39	35	36*	14
Card 2	3	1	1	0	7	1	22
Card 3	0	0	0	5	6	0†	0
Card 4	0	1	1	6	1	1	2
Card 5	0	0	8	1	0	0	3
No. of insects not under a card	21	12	8	5	7	18	15

*Formerly Card 3. †Formerly Card 1

Card 1 had beneath it 77 per cent. of the stationary insects. Since the insects tended to assemble under one card rather than others of presumably identical characteristics, it was concluded that in addition to being negatively phototactic *Petrobius* would form groups. The formation of such an aggregation could not be observed on account of the narrowness of the space beneath the card.

Group Formation

A smaller tank (15·5″ × 10″ × 11″ high), made of 0·25″ thick glass, was used in these experiments. Illumination was from one side. A 40-watt pearl bulb was placed approximately 15″ above each of two corners of the tank; the two lamps provided strong illumination in all corners and so deterred specimens from moving into them. The floor was covered with graph paper graduated in 0·5″ squares and held in position by transparent adhesive. Five 2″ square Bristol Board cards were arranged in a row parallel to and within 0·75″ of the longer wall of the aquarium and each one was held vertically by four small pieces of plasticine at its base. Behind the cards were a number of relatively dark areas. The quantity of shadow falling on the ground behind the cards visited according to a regular pattern (Fig. 2). The insects could be easily seen behind the cardboard screens. The experiments were carried out in September, 1955, in a dark room at a temperature of 18-19°C.

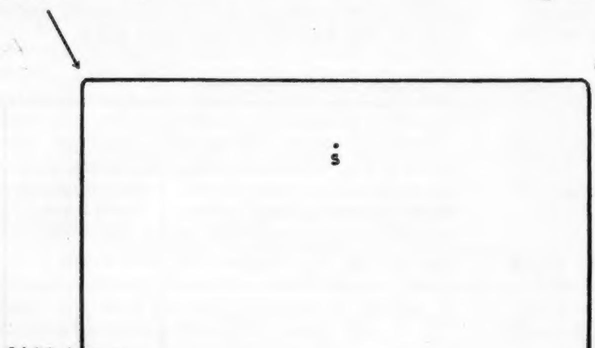
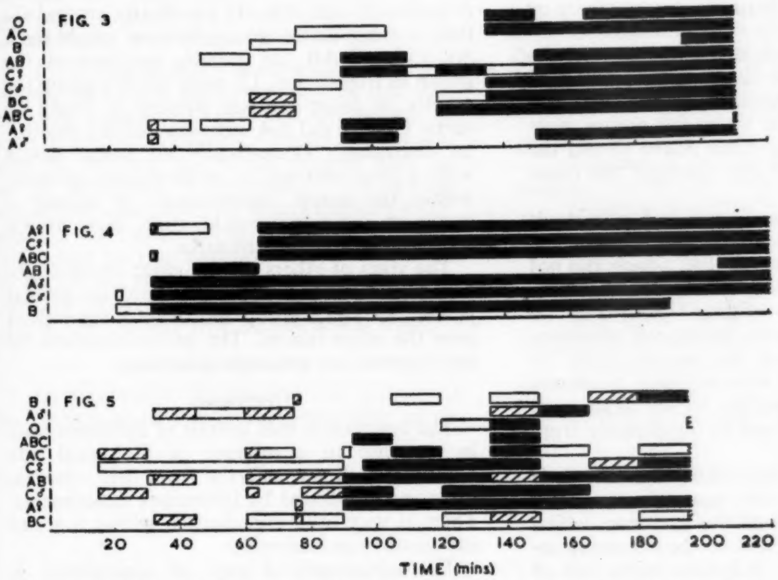


Fig. 2. Plan of the glass tank used in Experiments 8-12. Arrows indicate the positions of lamps. The dotted shading indicates the relative intensities of shadow falling on the floor of the tank behind the cards. S is the point of release of the insects.

Five experiments (Nos. 8-12) were undertaken; the last three will be reported in detail. Ten different, randomly selected insects were used in each experiment; the small number enabled a record to be kept of the position of each insect at various times. The duration of each experiment varied from 160 minutes to 220 minutes. The first two experiments were observed throughout their duration and the remainder only at approximately fifteen-minute intervals, although an individual observation may last for up to four minutes. In the latter experiments each insect was given a distinctive mark, by excising one or more of the three posterior processes. The left cercus was designated A, the central filament B, and the right cercus C. The letter assigned to any individual represented the caudal process removed; O represented the insect with no processes removed. This system provided eight possible combinations, viz., A, B, C, AB, AC, BC, ABC, and O. To obtain two more, and thereby the experimenal number of ten, A and C were subdivided into male and female. The removal of the processes did not appear to affect the activity of their owner. The ten insects were released simultaneously onto the floor of the tank at point S (Fig. 2) close to, and equidistant from, the two lamps.

The insects were very active in the early stages of the experiment, and some did not stop for a protracted period throughout their duration. They moved by running in short bursts, covering up to six inches of ground on each occasion. During movement, and afterwards when they remained still, the insects rotated their long antennae on either side and in front of their body. Jumping took place rarely, invariably off one of the cards. The cards were visited frequently and apparently equally on both sides. All other areas available to the insects were visited although there was a tendency for them to run in close proximity to the perimeter of the tank.

It was important to differentiate between a temporary halt and a long one; if an insect remained still for more than one minute and its antennae in that time moved little, it was regarded as being "stationary". The following terminology was adopted: "Base" referred to the area of the paper floor between the foot of a particular card and the



Figs. 3-5. Estimated time spent stationary by each insect in Experiments 10-12. White, cross-hatched and solid black blocks represent stationary insects that are isolated, in a minor group and in a major group respectively.

wall of the tank remote from the light source, thus "Base 1" referred to the area behind Card 1; "Card" referred to the surface of the card remote from the light source—throughout the experiments no insect was stationary on the side of a card facing the light.

Experiment 10—(Fig. 3). A group finally established itself at the junction of Card 2 with Base 2. In four other localities animals had remained stationary for short periods. The group fluctuated in size in its early stages and changed its composition during the first 120 minutes, after which time it increased fairly steadily in size. The ten insects were stationary for a total of approximately 830 minutes, for 121 of which they were not in a group.

Experiment 11 —(Fig. 4). B settled after 21 minutes on Card 5, was joined after 12 minutes by C♂ and A♂ and around these three a group of six individuals built up. Throughout this experiment BC and O were in constant motion. The other eight insects were stationary for a total of 1082 minutes; three (A♀, B and C♂) were stationary whilst outside the major group, but only for an estimated total of 24 minutes.

Experiment 12—(Fig. 5). The total time the ten insects were stationary was 844 minutes, but proportionately more stationary time was spent as solitary individuals (244 minutes=30 per cent.). The group never contained more than six members and after 195 minutes it was only four

Table II. Size and Location of Established Groups of *Petrobius brevistylis* Carp.

Experiment	Duration (min.)	No. of individuals in groups	Location of group	Area of substrate covered by group
8	160	9	Card 5	2 in. × 1 in.
9	190	5	Base 1 (near to Card 1)	1·5 in. × 0·5 in.
		4	Base 4 (near to Card 4)	1 in. × 0·5 in.
10	210	10 {7	Junction of Card 2	1 in. × 1 in.
		3	with Base 2	1 in. × 0·25 in.
11	220	6	Card 5	1 in. × 1 in.
12	195	4	Base 3	1 in. × 0·5 in.

strong. Stationary animals spent short periods at many sites, without forming groups of size or permanency.

The groups appeared at various sites in the tank, always under low illumination. Their size, situation and area of substrate covered are given in Table II. Two of the six major groups were established in the same place (Card 5) and the remainder dispersed evenly amongst the other bases and cards.

The groups occurring at bases had individuals aligning their body axes parallel to, and often alongside, the vertical cards. Individuals did not face any particular direction nor did any symmetrical arrangements display itself, and no group had all its members facing one direction. In the groups on cards no pattern could be recognised; the insects were arranged randomly with respect to one another, to the angle each made with the vertical and to the distance from the edge of the card.

Though the insects were close together, their bodies did not touch; they maintained contact almost exclusively through the antennae, which would rest on one or more of the adjoining individuals of the group and were rarely out of some contact. Apart from an occasional flicker the antennae remained quite motionless. They were brought to rest at no fixed angle from the head; frequently one pointed forwards and the other backwards. Thus each individual was in contact with two or more other members of the group.

Group initiation was observed on a number of occasions and appeared to be facilitated in one of two ways. The two individuals founding a group might both be moving until they came into antennal contact. (There was no evidence of the movement of one individual being directed towards another). A short period followed in which each individual moved its antennae over the surface of the other, particularly in the vicinity of the caudal processes and genitalia. They then became motionless although still maintaining contact through their antennae. Alternatively, one of the pair might be stationary at the time of contact and be joined by an actively moving individual. The same behaviour pattern then followed. Individuals coming into contact only became stationary on a minority of occasions. This was believed to be due to contact being made at a suitable time and situation.

Once initiated, the group did not require the presence of its founder members to maintain it. In Experiment 10, ABC and BC were displaced by C♂ within 15 minutes and this in its turn by A♂, A♀, C♀ and AB. It was finally around C♀ that a more stable group became established. A♀, C♂ and AB, the founder members of the group in Experiment 12, each left the group for greater or lesser periods without it losing its unity. Groups did not form around any particu‘ar individual. Occasionally an insect would walk a short distance to an alternative position within the group. Immediately on joining a group an individual would often draw its antennae through its mouthparts.

The visits of others had no effect on an established group. On several occasions an animal passed through a group and in so doing walked over the other insects. The group members did not respond but remained quite still.

Discussion

The conclusion that groups of *Petrobius* arise in response to a mixture of biological and abiotic stimuli was inferred from field observations and confirmed by laboratory experiments. There is very little organisation within a group and no obvious leadership.

The advantages, if any, of aggregation in *Petrobius* remain a matter of conjecture. Protection may be furnished from predators; in a group these insects are immobile, sudden activity by one member may be transferred rapidly as a result of mutual contact to the rest of the group, and rapid dispersion follows. As *Petrobius* may be inactive when solitary as well as when in a group, the aggregations cannot be classified as the "sleep" aggregations of Allee (1931).

Lhotse (1944) described group formation and measured its effects in *Forficula auricularia* L. Attraction between individuals takes place, as in *Petrobius*, without reference to sexual phenomena. The daily activity rhythm of these insects also appears to resemble that of *Petrobius*. A nocturnal period of active, isolated feeding is followed by a diurnal grouped one. There appears to be a close resemblance between the subsocial behaviour of the two species.

Summary

1. It was observed, during field collecting, that *Petrobius brevistylis* Carpenter (Thysanura, Machilidae) formed closely packed aggregations.

2. In the first series of experiments 56 individuals of *Petrobius* moved beneath cards and away from a bright light source immediately above them; they did not disperse randomly

amongst the cards available to them; dense aggregations were found under certain cards and the remainder were almost unpopulated.

3. In the second series of experiments marked animals were used. Light was applied laterally, the cards placed vertically, and the process of group formation witnessed. Groups appeared to form in response to abiotic stimuli and the mutual attraction of individuals. The groups were distributed randomly within the sites available and their members displayed no particular orientation to one another. Groups were not dependent on any particular member to maintain their integrity nor was there any apparent form of hierarchical organisation within them.

Acknowledgments

I am indebted to Professor L. A. Harvey of the University of Exeter for permitting me to carry out the second series of experiments in his laboratories after I had ceased to be a member of his Department. I am also grateful to the late Dr. W. C. Allee for helpful discussion in connection with this work.

REFERENCES

Allee, W. C. (1931). *Animal aggregations*. Chicago: University of Chicago Press.

Deegener, P. (1918). *Die Formen der Vergellschaftung im Tierreiche. Ein systematisch-soziologischen Versuch.* Leipzig: Veit.

Lhotse, J. (1944). L' "effet de groupe" chez *Forficula auricularia* L. *Bull. Soc. zool. Fr.*, **69**, 97-105.

Lie-Pettersen, O. J. (1907). Zur Kenntnis der Apterygotenfauna der nördlichen Norwegens. *Tromsø Mus. Aarsh.*, **28**, 51-76.

Wygodzinsky, P. W. (1941). Beiträge zur Kenntnis der Diplura und Thysanuren der Schweiz. *Denkschr. schweiz naturf. Ges.*, **74**, 113-227.

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PRELIMINARY OBSERVATIONS ON THE BEHAVIOUR OF THE ADULT WHEAT BULB FLY, *Leptohylemyia coarctata* (Fall.) USING THE "FIELD-CAGE-MARKING" TECHNIQUE

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Gough (1946) and Long (1958), using standardised sweeping technique studied the distribution and behaviour of the adult Wheat Bulb Fly in the field. They both recognised the inadequacies of the sweeping technique, and Long attempted to develop trapping methods which could be used instead. These, however, were not successful.

An attempt was made therefore to study behaviour by using the "field-cage-marking" technique first used during the summer of 1956 to investigate emergence and longevity (Dobson, Stephenson & Lofty, 1958). Preliminary observations were made for two 24-hour periods in July, 1957, (from 15.00 hours G.M.T. on 9th and from 13.00 hours on 15th) during the course of a second series of observations on emergence and longevity. The same cage and population of flies were used for both studies.

Methods

The cage, 24 ft. × 12 ft. × 6 ft. high, was constructed of Terylene netting of mesh 18 holes per inch supported on a metal framework. It was erected in a crop of winter wheat (var. Cappelle) on Pennell's Piece at Rothamsted in early June shortly before the flies started to emerge. To avoid unnecessary damage to the plants paths were cut through the wheat inside the cage.

Most of the flies used in the experiment were obtained from pupae collected locally and stored in muslin-covered pots of soil kept near the cage. The rest were collected inside the cage itself. Every day, the new emergences were marked, after immobilisation by chilling, with three spots of nitrocellulose paint applied to the dorsum of the thorax in such a way that each individual could be distinguished. The marked flies were then placed in an open topped container in the cage, and any unable to escape from this were killed and removed.

For the observations on behaviour the cage was marked out into thirty-two sections of one square yard each and these were searched for flies in the same order every hour. The identity, position, posture and activity of each fly seen was recorded, and to avoid disturbing the flies, care was taken not to touch either the cage or the plants. At night, searching was carried out with the aid of an electric torch. This did not disturb the flies unless it was directed on them for several seconds at close range, but, in its light, interpretation of the colour marks was sometimes difficult so that a few individuals could not be identified.

Maximum and minimum air temperatures at ground level were recorded hourly in the cage, and continuous records of total radiation were made at the Meteorological Station half a mile away.

Results

(1) Numbers of Flies Observed

From the longevity studies it was estimated that during the first 24-hour period the cage contained 86 female flies whose mean age on 9th July was 19·3 days (S.D. 4·3 days) and 20 male flies of mean age 18·2 days (S.D. 4·8 days). All of these, and also three unidentifiable individuals of each sex were found (Fig. 1). During the second period it was estimated that there were 37 female and 11 male flies in the cage and all except two of the females were seen. The mean ages on July 15th were 25·8 days (S.D. 3·6 days) for females, and 26·4 days (S.D. 4·2 days) for males.

Only a proportion of the total number of flies, varying from 29 to 55 out of 112 (mean 40·8 = 36·4 per cent.) on 9th and 10th July, and from 11 to 32 out of 46 (mean 19·4 = 42·2 per cent.) on 15th and 16th July was seen each hour (Figs. 1 and 2). The proportion might have been increased by searching the plants more thoroughly but this could not have been done without disturbing the flies.

(2) Positions of Flies in Cage

Flies were found on the walls and roof of the cage, on the plants and on the ground (Table I). A greater proportion of females than of males was found on the walls and roof during both

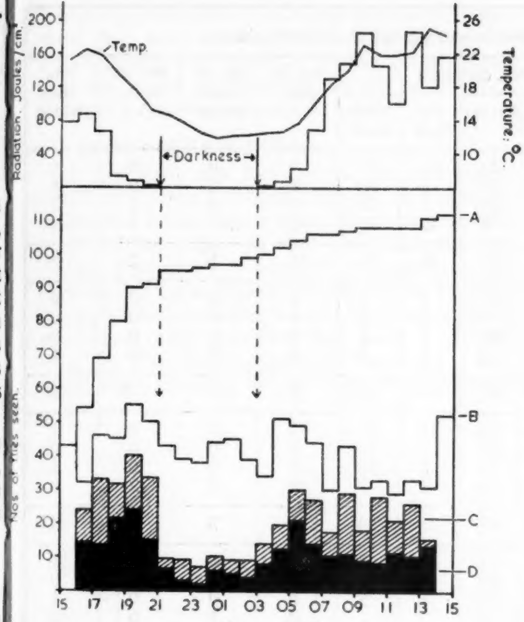

Fig. 1. Mean temperature, total radiation and numbers of flies seen on 9th-10th July, 1957. A. Accumulated total of different flies seen from hour to hour. B. Total number of flies seen each hour. C. Number of flies showing small movements during each hour. D. Number of flies showing large movements during each hour.

periods of observations, and proportionately more flies were found on the cage on 9th-10th July than on 15th-16th. This part of the population does not, of course, occur naturally and cannot be interpreted fully. Long (1958) showed that females disperse more than males, and this difference in habit possibly leads to the higher proportion of females than of males observed on the cage. At times, and most noticeably during the two or three hours before nightfall on 9th-10th July, many females were very active and flew repeatedly against the walls and roof; the males, however, did not behave thus, and were mostly found on the wheat plants. During the hours of darkness many flies were observed quiescent on the walls and roof of the cage. In natural circumstances these might have rested on the wheat plants, but equally well they might have been on other crops, hedgerows, trees, etc., to which they are known to migrate (Gough, 1946; Long, 1958). At present the greater pro-

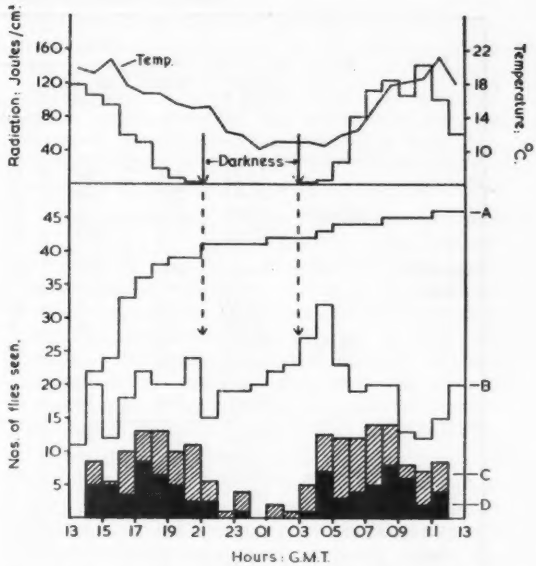

Fig. 2. Mean temperature, total radiation and numbers of flies seen on 15th-16th July, 1957. A. Accumulated total of different flies seen from hour to hour. B. Total number of flies seen each hour. C. Number of flies showing small movements during each hour. D. Number of flies showing large movements during each hour.

portions of both sexes found on the cage on 9th-10th than on 15th-16th cannot be explained.

The majority of the remaining flies were found on the wheat and on the ears and leaves of flowering grasses. Very few were found on the various weeds which included *Acinos arvensis* (Lam.) Dandy; *Veronica agrestis* L.; *Anagallis arvensis* L.; *Papaver rhoeas* L.; *Viola arvensis* Murr.; *Vicia sativa* L.; *Sinapis arvensis* L.; *Anthemis arvensis* L. and *Myosotis arvensis* (L.) Hill, although some of them, e.g. *Anthemis*, were very abundant. It is likely therefore that these plants were not attractive to the flies. Females were found in approximately equal numbers on the ears and leaves of the wheat plants but were seen less frequently on the stalks. The males, however, were most frequent on the ears and were comparatively infrequent on the stalks and leaves. This agrees with the suggestion of Long (1958) that females tend to go deeper into the crop than do males.

(3) Activity of Flies

Individual flies were not watched continuously so only the numbers known to have been active

Table I. Numbers of Observations on Flies in Different Places

Date	Sex	Numbers of observations on flies in different places										
		Time G.M.T.	Total	No. on cage	No. on wheat				No. on grass	No. on other plants	No. on soil	No. elsewhere
					Total	On ear	On Stalk	On Leaf				
9th-10th July	Female	15-21	245	199	42	14	11	17	4	0	0	0
		21-03	232	170	54	25	3	26	8	0	0	0
		03-09	236	178	53	26	6	21	3	0	1	1
		09-15	194	155	33	8	10	15	2	1	1	1
		Total	907	702	182	73	30	79	17	1	2	3
	Male	15-21	52	9	43	37	3	3	0	0	0	0
		21-03	22	14	8	6	0	2	0	0	0	0
		03-09	38	17	21	12	4	5	0	0	0	0
		09-15	28	14	13	6	1	6	0	0	0	1
		Total	140	54	85	61	8	16	0	0	0	1
15th-16th July	Female	13-21	120	62	55	31	10	14	2	0	0	1
		21-03	93	35	57	22	2	33	1	0	0	0
		03-09	117	41	73	33	8	32	1	0	0	2
		09-13	45	29	9	1	1	7	2	3	2	0
		Total	375	167	194	87	21	86	6	3	2	3
	Male	13-21	40	10	29	21	5	3	0	0	0	1
		21-03	26	6	20	20	0	0	0	0	0	0
		03-09	30	4	25	14	6	5	0	0	0	1
		09-13	17	7	9	6	2	1	0	1	0	0
		Total	113	27	83	61	13	9	0	1	0	2

during each hour can be compared. Flies were recorded as active when they were observed moving and when they changed position between one observation and the next. Minor movements such as changes in posture, and movements which were thought to have been caused by accidental disturbance were disregarded. Two classes of activity were distinguished; smaller movements, presumably involving walking, jumping or short flights, in which the flies remained in the same section of the cage (i.e. square yard) between one observation and the next, and larger movements in which the flies moved from one section to another. A high proportion of these larger movements almost certainly involved flight.

In recording activity, flies were classed as active or inactive during each hour and those making small movements only were distinguished from those moving longer distances. Movements which occurred between hourly observations were allocated to a particular hour according to a fixed convention. The results, are shown in Figs. 1 and 2 along with records of mean temperature at ground level and of total radiation. Males and females behaved similarly and are therefore grouped together. (Records for the first and last hours of each period are incomplete because the activity recorded for each hour depends partly on the observations made during the hours before and after it. They have therefore been omitted.)

These data are too few to permit detailed correlation of activity and weather conditions, but certain conclusions may be drawn. There was a sharp reduction of activity at nightfall and a resumption at daybreak. The presence or absence of daylight, rather than temperature, appeared to be the controlling influence during these particular observations. During the hours of darkness activity was not entirely inhibited and on 9th-10th an appreciable number of larger movements occurred. The night of 15-16th was colder than that of 9th-10th, and although smaller movements still occurred there were practically no larger ones. Temperatures on both nights were close to the threshold temperature for flight estimated by Long (1958) to be 12° to 13°C.

Although only a fraction of the total population was observed to be active at any one time, most flies were active at some time during the observations. On 9th-10th, 97 out of 112 (86·6 per cent.); and on 15th-16th, 42 out of 46 (91·3 per cent.) flies were classed as active.

(4) Posture of Resting Flies

At nightfall, most flies came to rest and many could be seen in exposed positions on the ears, stalks and leaves of the wheat plants and on the walls of the cage. At first they adopted the "head downwards" position characteristic of flies resting on a sloping surface during the day (Gough, 1946) but after a while they turned head uppermost and remained thus until daybreak (Fig. 3). The "head uppermost" attitude is unusual among resting Wheat Bulb Flies at other

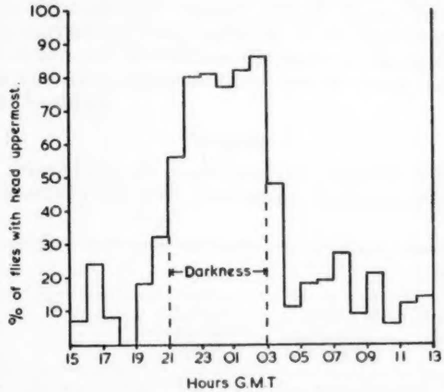

Fig. 3. Percentage of flies observed each hour resting head uppermost. Data for 9-10th July and 15th-16th July combined.

times, and appears to be a sleeping posture. (The flies also adopt a head uppermost posture when it is raining heavily during the day-time. They do not, however, become quiescent and will readily take flight. Flies in this condition could be roused and made to move by shining a strong light on them, but they became quiescent once more when the light was removed.

Discussion

The technique described here is believed to be a new method of studying the behaviour of an insect in the field. It has two principal advantages over other methods. The population under study is of known size and remains constant so that the worth of any particular observation can be evaluated by reference to the proportion of the population on which it is based. Secondly, the age of every individual in the population is known exactly. Although developed to study Wheat Bulb Fly, it could clearly be used for other species provided that individuals could be marked for identification and that their behaviour was not materially affected by the restriction of movement caused by the cage.

The present data, obtained during two periods of 24 hours each, are of limited scope, and no attempt has been made to make a detailed analysis. Clearly, with more extensive observations information on the behaviour of flies in different weather conditions, and on that of the two sexes at different ages and in different physiological states could be obtained. The system should also prove suitable for making continuous observations on the behaviour of individuals.

One of the main faults of the present data was that only a low proportion of flies was seen during each round of observation. This led to the loss of much information; for instance, a study of directional movements depends upon the same flies being seen in consecutive observations and in the present work the data obtained were quite inadequate. It is hoped that in future work this difficulty may be partly overcome by planning the layout of wheat and paths in the cage in such a way that it would be possible to inspect all plants without touching or disturbing them.

Summary

Preliminary observations on behaviour of Wheat Bulb Fly were made over two 24-hour periods during July, 1957, using individually marked flies confined in a large field cage standing in a wheat crop. Flies were observed on the fabric of the cage, on the wheat, on flowering grasses, and less frequently on various weeds (some of which were abundant) and on the ground. Differences in the proportions of the sexes on the cage and on various parts of the wheat plants reflected differences in their behaviour.

Females were very active shortly before nightfall, but after dark both sexes became quiescent (although some activity including flight persisted) and adopted a characteristic "head-upward" posture. At day-break, activity was resumed.

The results suggest that with development, the technique may prove a valuable means of studying behaviour under field conditions.

Acknowledgments

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REFERENCES

Dobson, R. M., Stephenson, J. W. & Lofty, J. R. (1958). A quantitative study of a population of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.) in the field. *Bull. ent. Res.*, **49**, 95-111.

Gough, H. C. (1946). Studies on Wheat Bulb Fly (*Leptohylemyia coarctata* (Fall.)) I. Biology. *Bull. ent. Res.*, **37**, 251-271.

Long, D. B. (1958). Field observations on the adult Wheat Bulb Fly (*Leptohylemyia coarctata* (Fall.)) *Bull. ent. Res.*, **49**, 77-94.

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REPRODUCTION IN *Physa pomilia* AND *Helisoma duryi**

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In some hermaphroditic gastropods age at time of egg production and number and viability of eggs produced per individual have been found to vary depending upon whether or not the opportunity for cross-fertilisation exists. The pattern of egg production and total life span of parent snails are also affected (DeWitt, 1954, 1954a; DeWitt & Sloan, 1958). Results of studies on two additional species of pulmonate snails are reported in this paper.

Determination of such relations is possible only under laboratory conditions. Since daily time-consuming observations of snails and eggs are required over a period of many days (790 in one instance), it is practicable to use only small numbers of individuals. Because of the small sample size, generalisations can be made only with caution.

Methods

Procedures in handling the animals were essentially the same as used in previous studies (DeWitt, 1954). Individuals from the same egg mass were either isolated or paired a short time after hatching. They were kept in aerated spring water and fed on a calcium alginate preparation throughout their life. Egg masses were removed from the parent container daily and records kept of the number of snails hatching from each mass (this number is used as a measure of viability). A complete life table is available for each isolate and each pair of snails. In the tables and figures, paired snails are indicated by P; isolated individuals by I.

The stock of *Physa pomilia* Conrad was obtained from streams in the Devil's Millhopper in Alachua County, Florida. *Helisoma duryi* Weatherby was obtained from the run of Manatee Spring in Levy County.

Results and Discussion

Physa pomilia

The paired individuals began laying eggs much earlier than did the isolates (Table I). This is favourable to the paired snails in the sense that their mean generation time, and thus the time to double the population, will be considerably less than that for isolated individuals. Similar circumstances were observed in *Physa gyrina* Say (DeWitt, 1954a) and in

Table I.

Physa pomilia						
	Age at oviposition (days)	Duration of egg-laying (days)	Post-productive period (days)	Life Span	Number eggs per snail	Viability (%)
I1	188	197	101	485	165	59
I2	161	387	139	686	340	77
I3	54	337	132	522	171	75
Mean	134	307	124	564	225	70
P1	35	346 & 451	100*	380 & 585	504	95
P2	37	163 & 191	5*	199 & 232	254	88
P3	37	422 & 543	82*	458 & 661	842	99
Mean	36	353	62	419	533	94

*for one snail only.

*This investigation was supported by a research grant E-1019 from the National Institutes of Health, Public Health Service.

Lymnaea columella Say (DeWitt & Sloan, 1958).

It is not known whether some stimulus provided by snails living together speeds up morphogenic development thus bringing gametes of pairs to an earlier maturation than those of isolates or whether early reproduction is a behavioural response. If the latter is the case, isolates may mature sexually as early as pairs but, due to a lack of stimulation provided, perhaps by copulation, do not lay eggs as early as the pairs

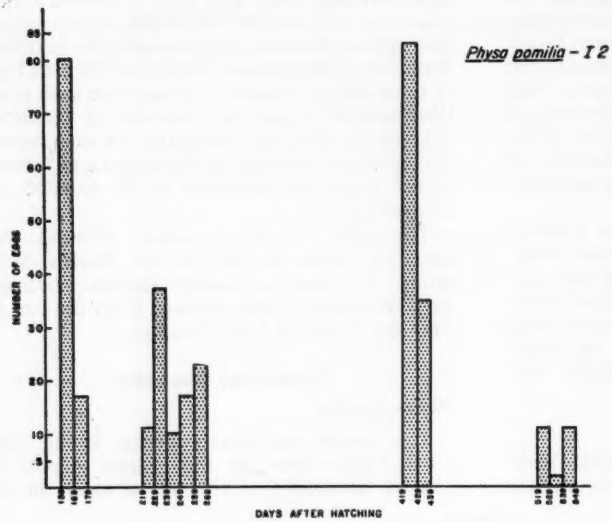

Fig. 1. The pattern of egg-laying in an isolated snail.

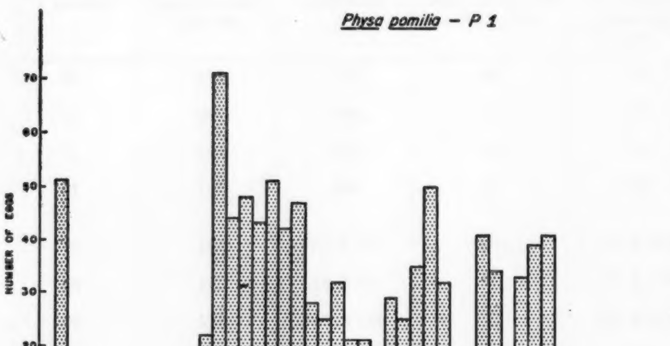

Fig. 2. The pattern of egg-laying in a pair of snails.

The mean viability of eggs produced by paired snails was considerably higher (94 per cent.) than that of isolates (70 per cent.). Self-fertilised eggs of *P. gyrina* were also less viable than those produced by individuals where the opportunity for cross-fertilisation existed (DeWitt, 1954).

Results were found to be somewhat different for *Lymnaea columella* (*loc. cit.*). The viability of eggs of isolates was 98 per cent. while that of pairs was 93 per cent. It might appear, from these results ,that *L. columella* could give rise to new populations with equal success under either set of circumstances. However, the pairs began egg production at an earlier date than the isolates and thus have a shorter generation time. If it can be assumed that the same effect operates in natural populations tions, then those with a shorter generation time would possess a distinct advantage when in competition with populations arising by self-fertilisation. Cain (1956) by the use of a genetic marker (albinism), has shown that in *Lymnaea stagnalis appressa* cross-fertilisation greatly exceeds self-fertilisation when there is an opportunity to cross-copulate.

In *P. gyrina* (*loc. cit.*) and *P. pomilia*, the number of eggs produced per individual appears to affect the total life span, those producing fewer eggs live a longer period of time.

The pattern of egg production for one isolate and one pair is shown in Figs. 1 and 2. The patterns are typical of the other snails used in this experiment and are similar to those of *P. gyrina* (DeWitt, 1954a). In both there is an

initial high level of egg production which is followed by a period of inactivity before further eggs are laid. The gaps between egg production are marked in the isolate (I 2). These gaps are not present in the pair (P 1) and this suggests that the paired snails are overlapping in the production of eggs.

Helisoma duryi

One isolate produced four eggs which did not hatch; the others did not lay any eggs (Table II). Crabb (1927) reared four individuals of *Helisoma* *trivolvis* in isolation for 377 days without their laying a single egg. However, his controls (paired individuals) did not produce any eggs during the same period of time. It is possible that, if he had kept them for a longer period of time, eggs might have been produced.

Two individuals (I 3 and I 4) isolated for 379 days without laying an egg, were paired on the 380th day and egg production began within a few hours. Together these snails produced a total of 2,552 eggs within a period of 301 days. Both of these individuals were sexually mature at the age of 380 days and apparently, the stimulus needed for egg-laying was provided by copulation.

Two other snails (P 2), paired shortly after hatching, produced a total of 1,485 eggs in 589 days. The third pair (P 1, also paired just after hatching) failed to lay any eggs.

There was no opportunity to observe the pattern of egg production in isolates. The pattern in pairs was similar to that of paired *Physa pomilia*.

Only two planorbids from North America, *Planorbis exacutis* (=*Promenetus exacuous*) and *Planorbis parvus* (=*Gyraulus parvus*), have been reported to be able to reproduce through self-fertilisation (Colton, 1918). There are no data available, however, for these species as to the numbers and viability of eggs produced by isolated individuals.

Table II.

Helisoma duryi			
Isolates			
	Number of eggs per snail		Life span (days)
I1	None		434
I2	4 on 647th day (did not hatch)		790
I3 & I4	None at end of 379th day		(Paired on 380th day. See below).
Pairs			
	Number of eggs per snail	Viability (%)	Life span (days)
P1	None	....	300 & 408
P2	743 (Began laying on 120th day)	61	491 & 783*
P3	1276 (Began laying on 380th day)	77	486 & 786**

*lived for 74 days after last egg mass laid.
**lived for 105 days after last egg mass laid.

Self-fertilisation is not uncommon among other aquatic snails. Many have been reported to be capable of reproducing in this manner (Brumpt, 1941).

Summary

On the basis of available information, the Lymnaeidae and Physidae are capable of reproducing through self-fertilisation; the Planorbidae are less successful. Although the first two families mentioned can reproduce in this manner the data indicate that this is not likely to be the general mode of reproduction since cross-copulation and hence cross-fertilisation is of benefit to the population.

REFERENCES

Brumpt, E. (1941). Observations biologiques diverses concernant *Australorbis glabratus*, hôte intermediarire de *Schistosoma mansoni*. *Ann. Parasit. hum. comp.*, **18**, 9-45.

Cain, G. L. (1956). Studies on cross-fertilisation and self-fertilisation in *Lymnaea stagnalis appressa* Say. *Biol. Bull.*, **111**, 45-52.

Colton, H. S. (1918). Self-fertilisation in the air breathing pond snails. *Biol. Bull.*, **35**, 48-49.

Crabb, E. D. (1927). The fertilisation process in the snail, *Lymnaea stagnalis appressa* Say. *Biol. Bull.*, **53**, 67-109.

DeWitt, R. M. (1954). Reproductive capacity in a pulmonate snail (*Physa gyrina* Say). *Amer. Nat.*, **88**, 159-164.

DeWitt, R. M. (1954a). The intrinsic rate of natural increase in a pond snail (*Physa gyrina* Say). *Amer. Nat.*, **88**, 353-359.

DeWitt, R. M. & Sloan, W. C. (1958). The innate capacity for increase in numbers in the pulmonate snail, *Lymnaea columella*. *Trans. Amer. micros. Soc.*, **77**, 290-294.

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THE TUBICOLOUS HABIT AND THE FIGHTING REACTIONS OF THE POLYCHAETE *Nereis pelagica*

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Aggressive behaviour towards other members of the same species has previously been reported in the polychaete *Nereis* (*Neanthes*) *caudata* Delle Chiaje (Herpin, 1923, 1926; Reish, 1957); a similar fighting reaction has now been observed in another species, *Nereis pelagica* (L.), when one worm attempts to occupy the tube in which another is living. The events occasioning this aggressive behaviour and the method of fighting have been observed over a period of several months in the laboratory during the course of experiments involving some 200 to 300 worms. As the circumstances of the fighting differ in important respects from those described in *Nereis caudata*, they are described in detail.

The Tubicolous Habit of *Nereis*

The Nereidae is conventionally regarded as a family of typically free-living or "errant" polychaetes, though in fact most species of *Nereis* live in a burrow or tube of some sort. Those which inhabit mud- or sand-banks, e.g. *Nereis diversicolor*, construct a gallery of burrows with several exits, the walls of the burrow are lined and consolidated with mucus, and the galleries have some degree of permanence, although the worms may desert them from time to time and construct new ones (Linke, 1939; Bogucki, 1953). A number of species which live under rocks may also construct a mucous tube which is attached to the surface of the stone (Hauenschild, 1956). Others, such as *Nereis pelagica*, which live in a similar environment, live in crevices but construct no tube. The degree of development of the mucus-gland system is correlated with the tube-building habits of the worms (Defretin, 1949).

Nereis is strongly thigmotactic. If a number of specimens of *Nereis pelagica* is placed in an aquarium, the worms aggregate in knots, particularly around detritus, pieces of seaweed or other debris in the tank. However, if they are provided with a number of lengths of glass tubing, the worms will distribute themselves between them. In all probability, once the worms are suitably accommodated in glass tubes they do not leave them unless they are subjected to some disturbance. Two individuals of this species kept in glass tubes in separate dishes have been under daily intermittent observation for more than two months and, so far as is known, have not left the tubes in that time. Similar habits have been observed in a variety of other species by a number of authors and are probably general in the Nereidae. In *Nereis virens* thigmotaxis is sufficiently strong to abolish the photonegative responses of the worms (Loeb, 1913), though not so in *Nereis diversicolor* (Herter, 1926).

All the maintenance activities are carried on in or from the tube. A respiratory current of water is drawn through the tube periodically (Lindroth, 1938; van Dam, 1937, 1938; Wells & Dales, 1951) and irrigation of the tube by dorsoventral undulations of the body is one of the most characteristic activities of the worms. Feeding is generally conducted from the mouth of the tube. Nereids appear to be omnivorous. Several species will take and eat animal material (Maxwell, 1897; Copeland & Wieman, 1924; Fauvel, 1923; Reish, 1954, 1957), including small worms and members of their own species. Several eat plant material (Gross, 1923; Reish, 1954) and Reish (1953) has reared *Nereis grubei* through two generations on a diet of dried mussel gonad and green algae. *Nereis diversicolor* has been observed on one occasion at least, to feed on suspended detritus which is filtered from the respiratory current of water in a mucus net (Harley, 1950). In most cases the worms do not leave the tubes for feeding, but extend not more than about one-third of the body from the mouth of the tube. In the sand-burrowing species *Nereis virens*, if food cannot be reached without extending further from the burrow, the worms will burrow under the sand to a position nearer the food (Copeland & Wieman, 1924). *Nereis japonica* is reported to emerge completely from its burrow for feeding (Izuka, 1908), but this appears to be quite exceptional. The only occasion on which most species certainly leave the burrow is when they are breeding. Reproduction generally occurs in the surface of the sea, but a few species breed in the tube. (Herpin, 1923, 1924, 1926, 1929; Smith, 1950; Rullier,

1950; Hauenschild, 1951; Durchon, 1955; Reish, 1957).

In common with the majority of tubicolous annelids, the most conspicuous and constant reactions of nereids to any kind of shock or disturbance is a sudden contraction of the longitudinal muscles and the very rapid withdrawal of the worm into its tube. This rapid defence responce is mediated by fast, longitudinal conduction pathways in the ventral nerve cord in the form of giant axons (Nicol, 1948; Bullock, 1948).

Thus although nereids show little sign of specialization to a tubicolous habit in their external morphology, the mucus glands and the nervous system show some of the features found developed to a much greater degree in the sedentary and more highly specialized tubicolous polychaetes. Even so, the daily pattern of activity of nereids centres around a permanent or semi-permanent burrow or tube and, even in a species such as *Nereis pelagica*, which normally lives under stones or in crevices, the same is true when it is provided with glass tubes in the aquarium. In nature there is presumably no shortage of suitable places where tubes or burrows may be formed, or crevices in which the worms may live. In the laboratory it is possible to provide conditions where there is some competition for tubes, and it is in these circumstances that fighting is most commonly seen.

Fighting During the Occupation of Tubes

The general procedure in these experiments has been for specimens of *Nereis pelagica*, between 10 and 20 cm. in length, to be accommodated in 20-cm. lengths of glass tubing of various internal diameters between 4 and 8 mm. In many cases the worms had entered and settled in the glass tubes in the storage aquarium, others were removed from the tubes they had adopted and placed in new ones at the start of the experiment. In the latter cases the worms settled down in the new tubes and stayed in them for at least several hours. Ten worms in tubes were placed side-by-side in a shallow pan of seawater for observation, Within about half an hour all resumed their normal pattern of activity. This consists of pumping water through the tube, crawling up and down it, contracting and extending, coming to the mouth of the tube and exploring the area within 2-3 cm. of the mouth of it, and reversing their direction in the tube. Judging by their behaviour when illuminated by dim daylight, they are in a state of almost continuous activity. Tubing of 6-8 mm. internal diameter is too wide for these worms; when fully contracted they are unable to block the tube, and irrigation of the tube can be achieved only by performing grossly exaggerated dorso-ventral undulations. Worms placed in tubes of this size spend much of their time moving up and down the tubes and reverse much more frequently than worms in narrower tubes. Eventually they leave the tube and crawl into others. For fully-grown worms, 5 mm., glass tubing appears to be the most satisfactory and they stay in it indefinitely. While they can and do stay in 4 mm. tubes for long periods, they have some difficulty in reversing in them and eventually desert them.

A worm that is unsatisfactorily accommodated for some reason (not always discernable), spends some time exploring the area around the mouth of its tube. Eventually it finds and enters the mouth of a neighbouring tube. If the tube is unoccupied it continues to crawl down it, but its posterior end remains in its original tube until at least half the body is inside the new one. However, if the new tube is already occupied, there is an encounter between the two worms, and this may take several forms.

(*a*) If the occupant does not react to the intruder, the latter sometimes crawls under it, does not attempt to evict it, and both worms live in the same tube. In this case the worms settle down at opposite ends of the tube, though if the tube is a wide one, they may lie on top of each other much of the time. Once two worms are settled in this way they tolerate each other without fighting and in the storage aquarium, where there is something of a shortage of tubes and about half the tubing has a wide bore, nearly a third of the worms are accommodated in this way. When the tubes have been under observation, it has been found that while two worms may settle in one tube for a time, eventually one of the worms leaves it.

(*b*) As the intruder starts to crawl into an occupied tube, the occupant nearly always crawls rapidly to the mouth of it. Contact between the occupant and the intruder is often sufficient to cause the latter to withdraw, particularly if the greater part of its body is still in its original tube. After this, the occupant usually remains at the mouth of its tube for 1-1½ minutes.

(*c*) When the original occupant is facing away from the intruder, the latter may crawl under it and the two worms stay in the tube without fighting. But quite often the intruder repeatedly bites the posterior end of the occupant, which of

course contracts and withdraws its tail abruptly, and drives it from the tube. Usually the occupant plays a less passive role than this. If the intruder should jar the tube as it enters it, or when when the intruder first bites the occupant, the latter immediately starts to reverse to face the intruder and fight back. This is rarely a successful manoeuvre. While it is reversing it is being bitten by the intruder and is retreating down the tube. Nearly always by the time it has reversed only a few anterior segments are still within the tube and it is impossible for it to evict the intruder from this position.

(*d*) If the occupant and intruder are facing each other and the intruder manages to crawl partly into the tube before the occupant reaches it, fighting usually ensues. This is conducted with one worm lying on its back so that the worms meet ventral surface to ventral surface. When the proboscis is everted, the jaws are inclined slightly downwards and this position for fighting facilitates the grasping of one worm by the other. The worms advance with the proboscis everted and grasp each other at the base of the proboscis or on the ventral surface of the anterior segments, often in the region of the sub-oesophageal ganglion. On the rare occasions that fighting takes place outside the tube, worms thrash vigorously when seized in this way, but in the confined space in the tube this is clearly impossible and the worm usually jerks back when bitten. Sometimes it bites back and the first worm often releases its grip, but occasionaly the worms remain locked together for a few seconds before separating. The worms separate after each attack and then, after a pause, lunge forwards again by a sudden contraction of the circular body-wall muscles. The probsocis frequently remains everted throughout the entire engagement. The tentacular cirri appear to play an important part in these encounters. They are directed forwards and, if they brush against its opponent, the worm reacts very suddenly, either by seizing it or by contracting and withdrawing. An intruder, by following the occupant as it withdraws, can invade the tube and drive the other out, or the worms may remain locked together by the jaws and push against each other. In either case the intruder seems always able to lodge in a tube, even if it does not evict the original occupant. Fighting continues at intervals of 15-30 seconds for 3-4 minutes. It stops either when the occupant has been pushed or driven out, or, more often, quite suddenly and without warning, before a decisive conclusion has been reached. The worms separate after one encounter, and the next time they advance, instead of seizing each other, one crawls under the other and they lie back to back. Only once has a decisive conclusion to a fight, which did not result in an eviction, been seen and that was when the intruder seized the occupant on the ventral surface in the region of the sub-oesophageal ganglion. The occupant immediately became extended and limp, it did not attempt to bite the intruder and when the latter released its hold, contracted slowly. The intruder then crawled under the occupant and no further fighting took place. Once the worms have stopped fighting and come to lie in this position, they remain still for anything up to five minutes and then each resumes its normal habits of crawling up and down the tube, reversing, and irrigating. Although they frequently come in contact with each other, often head-on, they do not fight again. On one occasion after 90 seconds fighting, the two worms settled down, lay quiescent for a time and then separated. After 6 minutes they approached each other again and resumed fighting with the result that the original occupant was pushed out of the tube. This resumption of fighting seems to be most exceptional. When fighting results in one worm or the other being driven from the tube, the present occupant comes to, and stays at the mouth of the tube for several minutes as soon as the fighting is over, and vigorously pumps a current of water over itself and through the tube for part of that time.

Fighting Outside the Tubes

Worms very frequently come into contact with one another outside the tubes without fighting. Worms not accommodated in tubes crawl over each other and even become tangled together in knots; worms in tubes investigate the area around the mouth of the tube and often come in contact with neighbouring worms doing the same thing. Occasionally they retract suddenly on brushing against each other, but more usually, they apparently ignore each other. On three occasions fighting has been observed outside the tube, and in each case it has either preceded or followed an attempt by one of the worms to invade another tube. These events are of some interest because they show, on the one hand, anticipatory behaviour, and, on the other, a continuation of the fighting reactions after the immediate stimulus evoking them had been withdrawn.

(*a*) Two worms, B and C, were in adjacent tubes, the latter in an 8 mm. tube which was plainly too wide for it to settle in comfortably. It spent 3½ hours in it, crawling up and down, and reversing much more frequently than other worms in narrower tubes. It and B were both extended 2-3 cm. from the mouths of their respective tubes exploring the area around them when C suddenly everted its proboscis and attempted to seize B. The latter withdrew sharply, everted its proboscis and advanced. Each worm seized the other at the base of the proboscis, after 3-4 seconds they parted and each retracted suddenly. Both worms then began to perform very rapid movements, advancing, weaving and retreating, much of the time with the proboscis everted and the jaws open. Whenever the tentacular cirri of one touched the other, the worm started away. When the worms attempted to seize each other, they bent on one side to attack, so that the ventral surface was presented to the opposing worm. After 30 seconds of this fencing, C grasped B by the proboscis and withdrew into its tube, dragging B 1-2 cm. into the tube after it. They became disengaged and B at once retracted into and down its own tube. Both B and C began vigorously to pump water through their tubes and continued to do so for about 60 seconds. Then C advanced and attempted to enter B's tube, but B advanced rapidly to the mouth of the tube and as soon as the two worms met, C retracted into its tube without attempting to attack. B continued to advance and followed C into its own tube and on making contact with C seized it on the ventral surface of the fifth segment. C struggled and then bit B on the ventral surface of the 15th segment. B at once broke off the engagement and retreated into its own tube. C made no further attempts to enter tube B.

(*b*) Thirty seconds after the previous encounter, C emerged again from its tube and after random searching movements, entered Tube A. The occupant of this tube came forwards to meet C and an inconclusive fight followed inside the tube, after which C and A settled in the tube together. In the course of this encounter between the two worms, C's body was stretched across the mouth of tube B. While C was engaged with A, B repeatedly emerged from its tube and attacked C. Its attacks ceased only when C had managed to insinuate a considerable part of its body into tube A and had withdrawn its posterior end from its original tube, so removing itself from the immediate vicinity of the mouth of B's tube. The attack by B started at least 60 seconds after the end of its own previous encounter with C, and it had suffered no particular disturbance by C in that interval.

(*c*) The only other occasions on which one worm has been observed to attack another outside the tube has been after the invasion of a tube by one worm and the eviction of the original occupant. This has been seen three times. The evicted worm has swum or crawled around the dish and within two or three minutes has begun to crawl over and past the mouth of the tubes. In each case the new occupant has emerged and attacked the other worm which has then crawled or swum away. On none of these occasions has the evicted worm attempted to enter any tube and the aggressor has not attacked other worms in the vicinity although there was opportunity to do so.

In the course of fighting the worms inflict considerable wounds on each other. One worm, after an encounter with two others, *seriatim*, had had seven serious lesions inflicted upon it: one across the dorsal surface of the peristomium, another across the dorsal surface of the 20th segment, others less serious, on the dorsal surface of other segments along the body and at the top of the parapodia, and three serious lesions on the ventral surface beside the ventral nerve cord. Another worm also received seven wounds on various parts of the body, while a third had a parapodium torn off. Lesions on the body wall do not appear to penetrate far beneath the epidermis, and the muscular body-wall can be seen protruding through the cut. Lesions of this sort evidently take several days to heal, since they were all macroscopically visible for the four days after the engagement that the worms were under observation.

Discussion

The method of fighting in *Nereis pelagica* is similar to that reported in *N. caudata* by Herpin (1923, 1926) and Reish (1957). In both species fighting consists of a series of brief engagements, each lasting a few seconds, repeated over a period of several minutes. However, the three other features of fighting in *N. caudata* that have been described apparently form no part of the aggressive behaviour of *N. pelagica*.

In *N. caudata* fighting is not specifically related to the occupation of tubes and takes place whether the worms are in them or not, but in *N. pelagica* fighting rarely occurs outside the

tubes and even then seems to be concerned with the occupation of them.

N. caudata fights members of its own, but not of the opposite sex. This behaviour is so dependable that Reish (1957) was able to sex the worms by observing their reactions when placed in a dish with a specimen of which the sex was known. The behaviour of the male is modified during the breeding season. *N. caudata* is one of the few species of *Nereis* which breeds in a tube and the male incubates the eggs. While it is doing so it will attack intruders of either sex. There is no evidence that fighting is in any way related to the sex of the worms in *N. pelagica* and fights have been observed between members of the same or opposite sexes.

Finally, *N. caudata* continues to fight until the stimulant of an opponent is removed and the worms become separated by one or two centimetres. In *N. pelagica* fighting continues for a certain length of time (3-4 minutes), unless one worm has been driven from the tube before then, and stops even though the two worms may still be in contact with each other.

Nereis is strongly thigmotactic and is inclined to crawl into any crevice, including the glass tubing that is presented to it. The behaviour displayed in the great majority of encounters between worms may be explained simply in terms of a thigmotaxis combined with an aggressive attitude towards other worms it may meet in the tube. However, the behaviour on a few, exceptional occasions, suggests that in fact such a simple explanation may be inadequate.

After the successful invasion of a tube by a worm and the displacement of the original occupant, the aggressive propensities of the new occupant of the tube may, on occasions, continue for as long as 6 or 7 minutes after fighting has ceased, and appear to be directed towards the previous occupant and not any other worm that happens to be in the vicinity and that it encounters. Furthermore, it may attack the previous occupant after some interval even though the latter makes no attempt to re-enter the tube. This implies that the worms are capable of distinguishing individuals with which they have previously fought. Although this rather unexpected conclusion is consistent with the observations, such behaviour is rare and it may be that these events are due to an unusual persistence of aggressive behaviour by the invading worm after it had evicted the original occupant of the tube, and that it attacked the latter and not other worms in the vicinity was due to chance or some other factor, and the fact that the worms had previously fought was coincidental.

On one occasion a worm anticipated its invasion of a neighbouring tube by attacking another worm when both were exploring the areas around the mouths of their respective tubes. Allowing, as the evidence shows, that fighting in *N. pelagica* is connected with tube-occupation, there is reason to suppose that the fighting in this instance anticipated the invasion of the tube, not that the latter was a consequence of the fighting. The aggressive worm was unsuitably accommodated in too wide a tube and spent much of its time exploring the area around the mouth of the tube as worms generally do before finding and invading other tubes. The behaviour of this worm differed from that of the others in that it attacked another worm before it had made contact with the tube of the latter.

These observations suggest that if the tube in which a worm is housed is unsatisfactory for some reason, it explores the area around the mouth of its tube and crawls into crevices or tubes that it may encounter, more readily than worms that are satisfactorily accommodated. Worms occupied in this way become aggressive and may fight other worms that they meet in the tubes they invade. On one occasion this aggressiveness appeared even before the worm had entered the new tube or had even located it. The occupant of the invaded tube generally attacks any other worm that enters it. Fighting lasts for a maximum of 3-4 minutes unless one worm is driven from the tube before then. Aggressiveness then disappears, as a rule, and two or more worms may live in the same tube. In exceptional cases aggressiveness may persist in a worm that has entered a tube and driven the original occupant out, and it then appears to be directed towards the previous antagonist, even though the worm has encountered other worms in the interval without fighting them.

Summary

Although the polychaete family Nereidae is not conventionally regarded as a tubicolous one, most of its members live in crevices, burrows or tubes and their general pattern of activity centres around the tube. This is true of *Nereis pelagica* which will live in glass tubes in the laboratory. If this worm is inadequately housed it invades neighbouring tubes, and if these are already occupied fighting between the invader and the occupant often ensues. The intruder seems generally able to lodge in the new tube. If

one or other worm has not been driven from the tube within 3-4 minutes fighting ceases abruptly and the two worms live in the tube. Exceptionally, aggressive behaviour by the successful invader may be resumed after an interval of several minutes and is apparently directed towards the previous occupant of the tube and not to other worms in the vicinity. On one occasion a worm anticipated its invasion of a tube by fighting a neighbouring worm outside the tube.

REFERENCES

Bogucki, M. (1953). Rozród i rozwoj wieloszczeta *Nereis diversicolor* (O. F. Muller) w Baltyku. (Reproduction and development of *N. diversicolor* in the Baltic.). *Polsk. Arch. Hydrobiol.*, **1**, 251-270.

Bullock, T. H. (1948). The physiological mapping of giant nerve fibre systems in polychaete annelids. *Physiol. Comp.*, **1**, 1-14.

Copeland, M. & Wieman, H. L. (1924). The chemical sense and feeding behaviour of *Nereis virens* Sars. *Biol. Bull. Woods* (*Hole*),

Defretin, R. (1949). Recherches sur la musculature des Néréidiens au cours de l'épitoquie, sur les glandes parapodiales et sur la spermiogénèse. *Ann. Inst. Oceanogr.* (*Monaco*), **24,47**, 231-238.

Durchon, M. (1955). Sur le polymorphisme présenté par quelques Néréidiens (Annélides Polychètes) au moment de la reproduction. *Bull. Soc. Hist. nat. Afr. N.*, **46**, 180-194.

Fauvel, P. (1923). *Polychètes Errantes* (Faune de France, **5**).

Gross, A. O. (1923). The feeding habits and chemical sense of *Nereis virens* Sars. *J. exp. Zool.*, **32**, 427-442.

Harley, M. B. (1950). The occurrence of a filter-feeding mechanism in the polychaete *Nereis diversicolor*. *Nature* (*Lond.*), **165**, 734. 117-257.

Hauenschild, C. (1951). Nachweis der sogenannten atoken Geschlechtsform des Polychaeten *Platynereis dumerilii* als eigente Art auf Grund Zuchtversuchen. *Zool. Jb. Abt. Physiol.*, **63**, 107- .

Hauenschild, C. (1956). Hormonale Hemmung der Geschlechtsreife und Metamorphose bei dem Polychaeten *Platynereis dumerilii*. *Z. Naturf.*, **11 b**, 125-132.

Herpin, R. (1923). Biologie et développement de *Nereis* (*Neanthes*) *caudata* Delle Chiaje. *C. R. Acad., Sci. Paris*, **177**, 542-544.

Herpin, R. (1924). La ponte et la développement chez quelques Néréidiens et Syllidiens. *C. R. Ass. Franc. Av. Sci.*, **47**, 558-562.

Herpin R. (1926). Recherches biologiques sur la réproduction et le développement de quelques Annélides Polychètes. *Bull. Soc. Sci. nat. Ouest*, iv, **5**, 1-250.

Herpin, R. (1929). Etude sur les essaimages des Annélides Polychètes. *Bull. biol.*, **63**, 85-94.

Herter, K. (1926). Versuche uber die Phototaxis von *Nereis diversicolor* O. F. Müller. *Z. vergl. Physiol.*, **4**, 103-141.

Izuka, A. (1908). On the breeding habits and development of *Nereis japonica* n.sp. *Annot. zool. Jap.*, **6**, 295-305.

Lindroth, A. (1938). Studien über die respiratorischen Mechanismen von *Nereis virens* Sars. *Zool. Bidr. Uppsala*, **17**, 367-497.

Linke, O. (1939). Die Biota das Jadebusenwattes. *Helgoland. wiss. Meeresunters.*, **1**, 201-348.

Loeb, J. (1913). Die Tropismen, in *Winterstein's Handb. Vergl. Physiol.*, **4**, 451-519.

Maxwell, S. S. (1897). Berträge zur Gehirnphysiologie der Anneliden. *Pflüg. Arch. ges. Physiol.*, **67**, 263-297.

Nicol, J. A. C. (1948). The giant axons of annelids. *Quart. Rev. Biol.*, **23**, 291-323.

Reish, D. J. (1953). Description of a new technique for rearing polychaetous annelids to sexual maturity. *Science*, **118**, 363-364.

Reish, D. J. (1954). The life history of the polychaetous annelid *Nereis grubei* (Kinberg). *Occ. Pap. Allan Hancock Fdn.*, **14**, 1-75.

Reish, D. J. (1957). The life history of the polychaetous annelid *Neanthes caudata* (Delle Chiaje), including a summary of development in the family Nereidae. *Pacific Sci.*, **11**, 216-288.

Rullier, F. (1950). Observations sur une ponte de *Platynereis dumerilii*. *Bull. Lab. marit.* (*Dinard*), **33**, 15-20.

Smith, R. I. (1950). Embryonic development of the viviparous polychaete *Neanthes lighti*. *J. Morph.*, **87**, 417-455

Van Dam, L. (1937). Uber die Atembewegungen und Atemvolumen von *Phryganea*-Larven, *Arenicola marina* und *Nereis virens*, sowie über die Sauerstoffausnotzung bei *Anodonta cygnaea*, *Arenicola marina* und *Nereis virens*. *Zool. Anz.*, **118**, 122-128.

Van Dam, L. (1938). *On the utilization of oxygen and the regulation of breathing in some aquatic animals* Groningen.

Wells, G. P. & Dales, R. P. (1951). Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *J. mar. biol. Ass. U.K.*, **29**, 661-680.

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LEARNING AND SOCIAL AGGREGATION IN LOCUST HOPPERS

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Introduction

Locusts vary considerably in morphology, behaviour and colour at different stages in their population cycle. When numbers are low, the individuals are generally scattered; the hoppers (nymphs) are green or fawn in colour and relatively inactive, and if they meet they do not stay together. During population peaks, when swarming takes place, the hoppers of the two species considered in this paper, *Locusta migratoria migratorioides* (R. & F.) and *Schistocerca gregaria* (Forsk.), have a black pattern, and in the later instars the background is bright yellow or orange; the distribution of the hoppers is discontinuous and they form bands that may contain many thousands of individuals. The hoppers of a band are so closely packed together that they spend a considerable part of the time in physical contact with one another. They stimulate each other to wander (march), and bands of *Schistocerca gregaria* often move a quarter of a mile or more a day (Ellis & Ashall, 1957). There are usually areas of country between hopper bands that contain no locusts and the cohesion of bands depends largely on the inter-attractions between individual hoppers.

Locusts from different types of population are so different in appearance that the true relationship between them was not realised until Uvarov (1921, 1928) put forward his phase theory of locusts. Faure (1932), using hopper colour and adult morphometric ratios as his criteria of phase, found that the various forms of locust could be produced in the laboratory by varying the density at which the individuals were reared. Locusts characteristic of scattered populations (phase *solitaria*) can only be produced in the laboratory if each individual is reared in isolation. Swarming-type locusts (phase *gregaria*) on the other hand are produced by rearing the hoppers in crowds. More recent work has shown that the two types of rearing condition also produce hoppers that vary in behaviour, in a similar way to those in the field (Ellis, 1951, 1953). Kennedy (1956) discusses modern ideas on phase in locusts and its importance in the understanding of natural populations.

In two carefully studied cases, gregarisation of scattered populations of locusts was found to result from an increase in the population followed by a restriction of the most suitable microhabitats, so that the individuals were forced together (Zolotarevsky, 1930, 1933; Maxwell-Darling, 1936). It is not known, however, whether outbreaks of locusts always follow the same pattern. Little consideration has been given to the reverse process, but a large reduction in numbers appears to play an important part in the transformation of a swarming population into a scattered one. Field workers also quote cases of small hopper bands having become dispersed by wandering into relatively large areas of dense, even vegetation (Kennedy, 1939; Johnston & Buxton, 1949; Ellis & Ashall, 1957; Chapman, in press). Under these conditions, the hoppers seem unable to continue to influence one another.

Since Faure's (1932) original experiments, various attempts have been made to analyse the types of hopper interaction that are responsible for phase change. It is unfortunate that quantitative work in the past has been concerned with colour and morphometric ratios, since changes in them can only take place when gregarisation has already commenced. The fact that gregarisation involves a number of processes that follow each other in a regular sequence appears frequently to have been overlooked. The definition of phase change has often been debated, and attempts have been made to restrict it to one aspect, such as colour or behaviour. Such restrictions are not in accord with the original definition (Uvarov, 1921, 1928) and also seem unnecessary, but since the complete change in phase from one extreme to the other occupies more than one generation, and influences the individual locust in numerous ways, agreement will never be easy.

Uvarov (1937) suggested a sequence of changes during gregarisation and Kennedy (1939) was able to confirm and elaborate this by the results of field studies on a scattered population of *Schistocerca gregaria*. Firstly, the locusts become concentrated, either by an increase in numbers or by a reduction of suitable habitats,

or both. During concentration they come into contact with one another and there follows a period when fairly quiescent groups are formed, especially during such activities as basking. It is during this period that their behaviour changes so that they develop positive attractions towards one another which tend to keep them in groups when the original concentrating factors are removed. Grouping that results from interattraction, as opposed to a patchy environment, has been called social aggregation by Ellis (1953). Although Uvarov pointed out in 1937 that the process by which formerly scattered locusts become "attuned" to each other, so that they stay together in groups, is an important stage of the gregarisation process, no experiments have been reported, beyond some field work by Volkonsky (1942), who claimed that mutual olfactory stimulation helped to bring hoppers together during the earlier stages of gregarisation, and was replaced later by visual stimuli. Both Uvarov (1928) and Kennedy (1939) favoured a visual conditioning or habituation of one locust to its neighbours, so that eventually each individual tended to keep within visual range of others of its species. Unfortunately, this hypothesis has not been tested experimentally. Once the locusts have learned to aggregate socially, further mutual stimulation leads to an over-all increase in activity and marching takes place. Kennedy rightly pointed out that the greater activity that is so characteristic of swarming hoppers must be one of the later stages in gregarisation. Hoppers must first become habituated to one another so that they stay together in groups, otherwise increased activity will simply lead to re-dispersal. Colour changes in hoppers may be fairly rapid, especially in *Schistocerca* (Stower, *in press*). Changes in morphometric ratios only take place after some time has been spent living in bands.

The present paper concerns the changes that take place in the behaviour of previously isolated hoppers (assumed to be similar to phase *solitaria* hoppers in the field) when, as the result of being forced to live together, they learn to aggregate socially with one another. Previous laboratory work has shown that the change is a rapid one, differences in behaviour being measurable after a few hours of crowding (Ellis, 1953). Once the ability to aggregate socially has been acquired, it is not so readily lost, although prolonged isolation of the hoppers eventually results in the loss of it. Newly hatched hoppers do not group well and a considerable degree of learning to aggregate socially takes place at each generation (Ellis, 1956) under suitable conditions. However, the maximum amount of grouping shown by hoppers after training is influenced by hereditary factors, for hoppers from crowded parents group more than those from isolated parents (unpublished data; also Ellis, 1953, and Kennedy, 1956).

Material and Methods

The Locusts

Hoppers of two species were used in experiments, namely the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.) and the Desert Locust, *Schistocerca gregaria* (Forsk.). They came from laboratory stocks reared crowded for many generations, and all of them were black at hatching. Measurements of behaviour were made when the hoppers were from 8-12 days old, in the middle of the second instar. In general, the method used was to rear the locusts in different ways from hatching until the time of testing. In all cases, except when hoppers were reared in crowds, the eggs were isolated just before hatching to ensure that no contact took place between the hoppers. The jars and boxes containing isolated hoppers were screened so that the hoppers could not see those in neighbouring containers. In this paper, the term *isolated hopper* means a locust reared in isolation in the way outlined above; the so-called *crowded hoppers* were reared with others of the same species in a crowd. The hoppers were fed on fresh grass, and during the day electric lamps provided extra heat and light.

There are always small seasonal variations in locust stocks in the laboratory. In each experiment, therefore, the hopper groups to be compared were reared at the same time and came from the same egg pods.

Measurement of Social Aggregation

The amount of attraction between hoppers was measured by testing the behaviour of small groups in a cage that provided a physically uniform environment. The hoppers could therefore form groups only as the result of mutual interattraction. The apparatus was similar to that previously used (Ellis, 1953). The experimental cage was ring-like (Fig. 1), with an external diameter of 12 inches (30·5 cm.) and an internal diameter of 6 inches (15·3 cm.). The cage walls were 2·5 inches (6·3 cm.) high and a sheet of glass formed the top. The internal walls were made of celluloid and the floor was of varnished paper. Walls and floor were washed over at the end of

each test. The cage was lit by a 100-watt lamp hung centrally 24 inches (61 cm.) above it. The lamp was surrounded by a large white shade that was 18 inches (48·8 cm.) tall and had a maximum diameter of 24 inches.

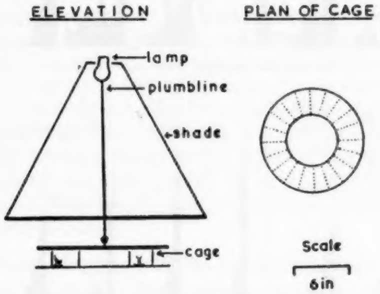

Fig. 1. Diagrams of the cage used to test social aggregation

The sides and floor of the cage were marked into 20 equal divisions (Fig. 1) and 10 hoppers, all of which had been reared in the same way, were placed together in the cage for test. The majority of experiments were carried out at an air temperature of 28°C. It has been shown that at this temperature *Locusta* hoppers take 20 minutes to settle down after being placed in the cage (Ellis, 1953), so the first reading was made after 30 minutes. *Schistocerca* hoppers require a similar period (unpublished observations). At each reading, the number of hoppers per cage division was recorded; such readings give a measure of the number of hoppers in groups. On the average, these readings give similar results to those in which the cage divisions are ignored and the hoppers are counted as grouped if they are within two hopper lengths of each other (Ellis, 1953). After the first reading, the hoppers were made to walk about, and were then allowed to settle for another 30 minutes before the second reading was taken. Four readings were made in this way with each batch of hoppers. Generally, four different groups of hoppers (a total of 40 individuals) were thus tested for each type of rearing condition.

The distribution of the hoppers in the cage to be expected by chance is given by the successive expressions of the binomial $(19/20 + 1/20)^{10}$. This is more correctly used than the Poisson distribution mentioned in Ellis (1953), although for this particular ratio of hoppers to cage divisions, the two distributions are very similar. Only non-gregarious grasshoppers and a proportion of isolated locust hoppers are randomly distributed in the apparatus (Ellis, 1953).

The results for the four tests with hoppers that had been reared in the same way were added (*i.e.* there were 160 hopper observations for each experiment, for each type of rearing). They are illustrated in histograms (Figs. 2-5) showing the numbers of hoppers that were alone in the cage divisions, the numbers in twos and so on, up to the numbers in tens per division. For comparing the results statistically the four readings per test were added. The number of hoppers in groups was then calculated and this was treated as a measure of social aggregation and was used in the statistical analysis. A similar analysis was made of the number of hoppers in groups of three and more, ignoring those in twos and those by themselves.

Hopper Colours

The colours of the hoppers at second instar were recorded and classified into a small number of types.

Locusta

Locusta hoppers have a variety of background colours and are speckled with spots of black or brown. The speckling becomes organised into a pattern, especially in phase *gregaria* hoppers (see type (*a*) below). Phase *solitaria* hoppers are green or fawn with little or no darker pattern (see type (*d*)).

(*a*) Typical of crowded hoppers. Face and lower part of thorax orange, often speckled with black. Pronotum black and dorsal surface of abdomen mainly black.

(*b*) Face and lower part of thorax lemon-orange or greenish-yellow. Rather less black pigment on the dorsal surface of the pronotum. Dorsal part of abdomen mainly black.

(*c*) Face and lower part of thorax different in colour from the rest of the body, generally some shade of yellow, green or pink-fawn. Dorsal part of thorax and abdomen grey, fawn or brown, with black longitudinal stripes on thorax or abdomen, or both.

(*d*) Typical of isolated hoppers. General colour uniform all over head and body, usually some shade of green, yellow-fawn, orange-fawn, pink-fawn or grey, but face and lower part of thorax paler. Brown or grey (rarely black) longitudinal stripes on pronotum, or abdomen, or both.

Extreme phase *solitaria* hoppers are green or fawn with practically no darker markings. This

type did not occur during the present experiments; only hoppers that are pale at hatching and are then reared isolated can be expected to produce such hoppers by the second instar (Hunter-Jones, 1958).

Schistocerca

Schistocerca hoppers from bands have a well defined black pattern (type (*a*)) that is reduced in phase *solitaria*. The background colours of the two phases are also different, phase *solitaria* generally being green (type (*d*)).

(*a*) Typical of crowded hoppers. Well developed black pattern, background cream over most of the body, but pinkish on thorax and head. Occipital patch (a small patch of colour just behind the eye) deep red-orange.

(*b*) Black pattern well developed, but rather less on pronotum and head. Background cream and occipital patch orange.

(*c*) Black pattern similar to (*b*) Background green or greenish. Occipital patch green or yellow.

(*d*) Frequent amongst isolated hoppers. Considerable loss of black pattern. Background green or greenish. Pattern sometimes mauvish or brown.

Again, the extreme *solitaria* colouring, in which there is little dark pattern, did not occur, for the reasons outlined above.

The percentages of experimental hoppers in the various colour classes are shown in the lower histograms in Figs. 3, 4 and 5.

Experiments and Results

1. Crowded and Isolated Hoppers

When placed in the aggregation cage, hoppers reared crowded behaved in a very different way from those reared isolated from birth. The results illustrated in Fig. 2, B and E, may be taken as examples; others are shown in Figs. 3, 4 and 5. Generally between 45 per cent. and 65 per cent. of isolated hoppers settled alone in the cage divisions and very few were in groups of four or more; in some of the tests with *Locusta*, the hoppers were distributed at random in the cage (Table I). Amongst crowded hoppers, some 80 per cent. grouped and many, especially in *Schistocerca*, were in groups of four and more; their distributions in the cage were always very different from the chance one (Table I) and significantly more of the crowded hoppers grouped than the isolated ones (Table II, i).

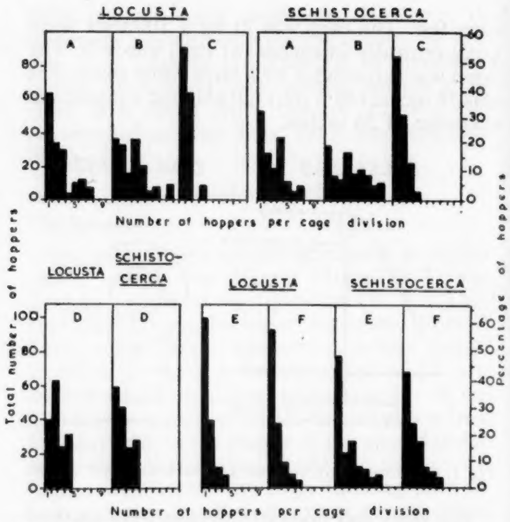

Fig. 2. Social aggregation in second-instar hoppers treated in various ways before being tested. A, B, C, D, hoppers reared crowded from hatching; E, F, hoppers reared isolated from hatching. A, antennae amputated on the evening before the test; B, normal hoppers; C, tested in the dark; D, tested in the dark, but with two-hour periods between readings. E, hoppers well fed up to the beginning of the test; F, hoppers starved for four hours before the test.

Table I. Comparing the Distribution of Hoppers within the Experimental Cage with that to be Expected by Chance. (The results for the four separate tests of each experiment have been added together. Degrees of freedom, 3; p=0·05 for chi-squared 7·815, and 0·01 for chi-squared 11·341. An asterisk indicates random distribution of the hoppers.)

Method of rearing	Reference to figures	Chi-squared	
		Locusta	*Schistocerca*
Isolated in jars	2E	2·103*	57·237
„ „ „	3A	16·767	30·448
„ „ „	4A	37·948	17·905
„ „ „	5A	3·356*	24·905
Crowded, but tested in darkness	C2	4·200*	8·089
Crowded in cages	2B	143·055	173·129
„ „ „	3E	164·287	209·310
Crowded 11 per jar	4D	136·197	122·137
Crowded 21 per jar	5C	124·675	182·290

2. Crowded Hoppers in Darkness

Crowded hoppers were tested in darkness, except for a very dim light used only to take the readings. Under these conditions grouping was reduced and the *Locusta* hoppers were distributed at random in the cage (Fig. 2 C, Table I). This suggests that in crowded hoppers visual stimuli play an important part in bringing the individuals together to form groups. However, if the hoppers are left in the cage for two hours before a reading is made there is some increase in grouping (Fig. 2 D), although it is still far below that for hoppers tested in the light. Presumably the hoppers can form groups in darkness only if by chance they touch each other while wandering about the cage.

3. Crowded Hoppers with the Antennae Amputated

When crowded locusts are basking in a group they continually touch each other with the antennae, and in face-to-face encounters they twirl their antennae at each other. Isolated locusts did not twirl their antennae when they were first put with other locusts, so it seemed reasonable to suppose that the antennae play some part in the interactions that lead to social aggregation. Crowded hoppers in which the antennae had been amputated during the evening before the day of the test were compared with normal individuals; the tests represented in Fig. 2, A and B, were carried out in pairs. Removing the antennae of the crowded hoppers reduced grouping by a small and possibly significant amount (Table II, ii).

4. Isolated Hoppers and Their General Activity

Isolated hoppers tend to be far less active than crowded ones and it is possible that this plays some part in the difference in the degrees of grouping in the experimental cage, because the hoppers must move about in order to meet each other. Since the activity of hoppers can be increased by starvation (Ellis, 1951; Ellis & Hoyle, 1954), isolated hoppers were starved for four hours before the test and their behaviour compared with that of others fed to the time of test in the normal way. This, however, did not alter social aggregation (Fig. 2, E and F; Table II, iii).

5. Visual Interactions and Learning to Aggregate

Visual interactions between locusts have generally been assumed to play a considerable part in the maintenance and formation of groups. Perhaps social aggregation depends on the locusts becoming habituated visually to one another as Uvarov (1928, 1937) and Kennedy (1939) suggested. Two experiments were carried out to test this hypothesis.

Fig. 3 shows the results of tests in which the behaviour of isolated hoppers reared in the normal way (A) was compared with that of isolated hoppers reared in jars with reflecting surfaces, so that the hoppers could see their own reflections (B). Although hoppers reared in the mirrored jars aggregated a little more than the others, the differences were not significant (Table II, iv). On the whole there were no large differences in colour.

In the second series of tests, hoppers were reared in small celluloid boxes measuring $2\frac{1}{2}$ in. $\times$ $2\frac{1}{2}$ in. $\times$ $1\frac{1}{2}$ in. ($6{\cdot}3 \times 6{\cdot}3 \times 3{\cdot}8$ cm.). Half of the boxes were placed in isolation, while the others were placed inside a cage full of hoppers. In the latter case the boxed

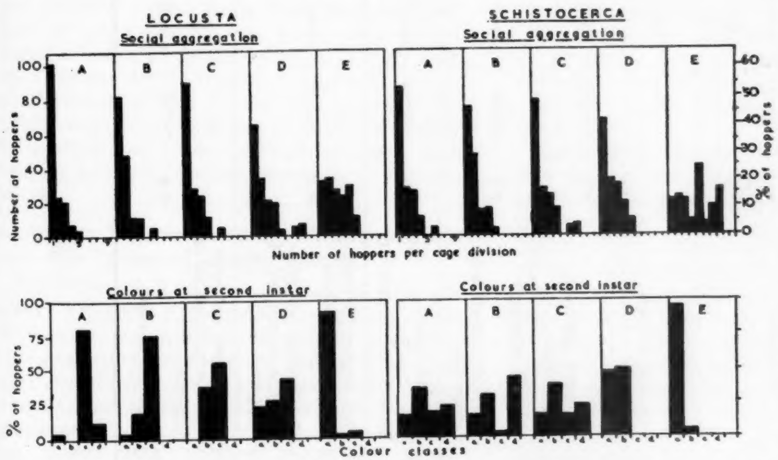

Fig. 3. Social aggregation and colours of second-instar hoppers reared in various ways from hatching until the time of the test. A, reared isolated; B, reared isolated in mirrored jars; C, isolated in small celluloid boxes; D, one hopper per celluloid box, placed in a cage full of hoppers of similar age; E, crowded in cages. (For explanation of colour classes, see text).

Table II. Comparing the Numbers of Hoppers Forming Groups in the Experimental Cage in Relation to Rearing Conditions
(The results for the four tests of each experiment have been added together); means are test means.

	Reference to figures	Rearing conditions for the two groups compared	*Locusta*						*Schistocerca*					
			Hoppers in groups of 2 and more			Hoppers in groups of 3 and more			Hoppers in groups of 2 and more			Hoppers in groups of 3 and more		
			Mean difference	t	p	Mean difference	t	p	Mean difference	t	p	Mean difference	t	p
i	2B, 2E	Isolated in jars. Crowded in cages.	16·3	7·2222	<0·01	18·3	5·3288	<0·01	11·5	3·8878	<0·01	13·0	3·7528	<0·01
ii	2A, 2B	Crowded.* Crowded, antennae amputated.	7·0	4·7551	<0·02	7·5	1·9753	>0·10	5·0	3·1624	>0·05	8·5	4·3894	<0·05
iii	2E, 2F	Isolated, well fed.* Isolated, starved 4 hr. before test.	1·5	3·000	>0·05	1·5	0·6765	>0·50	2·8	1·3644	>0·20	1·8	1·1714	>0·30
iv	3A, 3B	Isolated in jars. Isolated in mirrored jars	5·0	1·3779	>0·20	1·0	0·2907	>0·70	2·8	1·0112	>0·30	1·8	0·7012	>0·50
v	3C, 3D	One hopper per celluloid box in isolation. One hopper per celluloid box in cage full of hoppers.	6·3	2·2126	>0·05	4·8	1·3629	>0·20	2·8	0·7561	>0·40	1·8	0·4560	>0·60
vi	3D, 3E	One hopper per celluloid box in a cage full of hoppers. Crowded in cages.	8·0	2·5141	<0·05	8·0	2·2974	>0·05	12·0	5·6569	<0·01	14·5	5·4478	<0·01

*Tests done in pairs.

hoppers not only saw the others outside, but also received some olfactory and auditory stimuli from them as well because the celluloid boxes were not airtight. Placing the boxes inside the cage full of hoppers increased social aggregation in the boxed *Locusta* hoppers by only a small, non-significant, amount, and made no difference to the *Schistocerca* hoppers (Fig. 3, C and D; Table II, v). The amount of grouping shown by the hoppers reared in boxes in a crowd was considerably less than that for normal cage-crowded hoppers that were tested at the same time (Fig. 3, D and E; Table II, vi).

There was a small shift towards *a*-type coloration in hoppers of *Locusta* when the boxes were placed in a crowd and a large shift towards it in the case of *Schistocerca* (Fig. 3, C and D). Similar experiments with *Schistocerca* have been reported by Chauvin (1941) and Nickerson (1954). All of Chauvin's hoppers developed the full pattern of phase *gregaria*. Nickerson, on the other hand, found that the proportion of hoppers showing phase *gregaria* pattern was less for boxed hoppers placed in a crowd than for normally crowded ones.

The first experiment showed that a hopper able to see its own reflection during rearing behaved in a similar way to one reared isolated. The colours of the hoppers were also not greatly altered. In the second experiment, the hoppers that were reared in separate boxes placed in a cage full of locusts received visual, olfactory and auditory stimuli from those outside. Since these hoppers showed very poor social aggregation it seems likely that physical contact with other locusts during rearing is necessary for the development of this behaviour. On the other hand, visual plus olfactory plus auditory stimuli from other locusts brought about some shift towards *a*-type coloration, especially in *Schistocerca*.

6. Hoppers Reared Crowded with Grasshoppers or with Locusts of Another Species

Both Husain & Mathur (1936) and Chauvin (1941) reported experiments in which single *Schistocerca* hoppers were reared with groups of non-gregarious grasshoppers. Husain & Mathur used *Poecilocerus pictus* and species of *Chrotogonus*. Chauvin used *Acanthacris ruficornis*. The grasshoppers remained unchanged in colour, but the *Schistocerca* hoppers developed phase *gregaria* colouring. Husain & Mathur (1936) also crowded single locusts with house crickets, *Acheta domesticus*, but in this case the *Schistocerca* hoppers were phase *solitaria* in colour. They explained their results by suggesting that the grasshoppers increased the activity of the locusts and so caused a change in colour. The lack of *gregaria* colouring in hoppers reared with crickets was attributed to the fact that the two types of insect did not meet very often as the crickets were only active at night. They also tried various methods of increasing the activity of isolated hoppers by mechanical means and obtained phase *gregaria* coloration. However, it seems likely that their experimental hoppers were in visual contact with one another while being exercised, and their experiments have been criticised by Chauvin (1941), who was unable to repeat their results with a similar apparatus, and by Nickerson (1954).

As far as social aggregation is concerned, it is difficult to see how increased exercise by isolated hoppers could improve their powers of grouping when they are later placed with a number of other hoppers for the first time. The fact remains, however, that the non-gregarious grasshoppers were found by two groups of workers to affect hopper colours. Tests were therefore made in the course of the present work to see if the behaviour of locust hoppers could be altered by rearing them with grasshoppers. There were four methods of rearing, in all of which jars of 360 cc. capacity were used:

(*a*) One locust alone in a jar.

(*b*) One locust with ten nymphs of the non-gregarious grasshopper *Eyprepocnemis*.

(*c*) One locust with ten hoppers of another locust species, *i.e.* one *Locusta* with ten *Schistocerca* and one *Schistocerca* with ten *Locusta*.

(*d*) One locust with ten hoppers of the same species.

At the second-instar, groups of ten hoppers that had been reared in the same way were tested together in the experimental cage. The results are illustrated in Fig. 4. It is immediately evident that crowding locust hoppers with grasshoppers or with nymphs of other locust species produced similar social aggregation to crowding with the same species (Fig. 4, B, C and D; Table III, iii and iv). The hoppers that were reared in isolation grouped less than those reared crowded in jars with the same species (Fig. 4, A and D; Table III, i). The hoppers that were crowded with grasshoppers also grouped more than the isolated ones (Fig. 4, A and B; Table II, ii).

It should be noted that the nymphs of the grasshopper *Eyprepocnemis* are never gregarious and those reared crowded settle at random in the

Table III. Comparing the Numbers of Hoppers Forming Groups in the Experimental Cage in Relation to Rearing Conditions
(The results for the four tests of each experiment have been added together; means are test means)

	Reference to figures	Rearing conditions for the two groups compared	*Locusta*						*Schistocerca*					
			Hoppers in groups of 2 and more			Hoppersin groups of 3 and more			Hoppers in groups of 2 and more			Hoppers in groups of 3 and more		
			Mean difference	t	p	Mean difference	t	p	Mean difference	t	p	Mean difference	t	p
i	4A, 4D	Isolated in jars. Crowded 11 per jar.	10·0	4·0967	<0·01	13·0	4·7602	<0·01	9·8	4·7886	<0·01	12·3	2·2822	>0·05
ii	4A, 4B	Isolated in jars. 1 hopper + 10 grass-hoppers per jar.	10·3	2·6338	<0·05	8·3	2·7280	<0·05	9·8	7·6000	<0·01	9·3	3·5014	<0·02
iii	4B, 4D	1 hopper + 10 grass-hoppers per jar. 11 hoppers of same species per jar.	0·3	0·0732	>0·90	4·8	2·6782	<0·05	0	—	—	3·0	1·6860	>0·10
iv	4C, 4D	1 hopper + 10 of another locust species per jar. 11 hoppers of same species per jar.	0·3	0·1356	>0·80	1·8	0·6132	>0·50	0	—	—	1·5	0·277	>0·70
v	5A, 5B	Isolated in jars. 1 hopper + 20 wood-lice per jar.	13·0	5·8137	<0·01	11·5	4·2228	<0·01	8·5	4·1033	<0·01	8·5	2·4081	>0·05
vi	5B, 5C	1 hopper + 20 wood-lice per jar. 21 hoppers per jar.	3·8	1·7398	>0·10	3·8	1·1875	>0·10	5·0	3·0860	<0·05	8·0	2·7507	<0·05

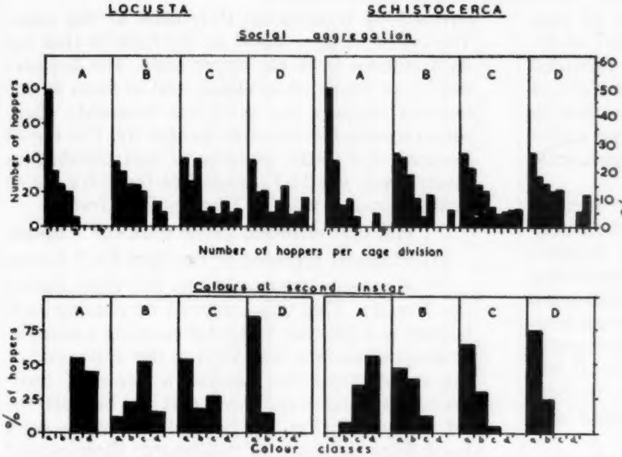

Fig. 4. Social aggregation and colours of second-instar hoppers reared in various ways in 360 cc. jars from hatching until the time of the test. A, isolated; B, one locust and ten grasshoppers per jar (see Fig. 5 D); C, one locust and ten hoppers of another locust species; D, 11 locusts of the same species. (For explanation of colour classes, see text).

aggregation cage ($\chi^2 = 7{\cdot}8086$, $P > 0{\cdot}05$, Fig. 5 D). That is, even when reared in crowds, the hoppers of *Eyprepocnemis* do not develop attraction to one another.

The results as regards the colour of the hoppers did not follow the same course as those for behaviour. Maximal *a*-type colouring was found only in those hoppers that were reared crowded with members of their own species, suggesting that a specific type of interaction is concerned in the phase change in colour. There were fewer hoppers of *a*-type colour when the hoppers had been reared with another locust species and still fewer when crowded with grasshoppers. The *Schistocerca* hoppers appeared to be more sensitive to crowding with grasshoppers as far as colour was concerned than did the *Locusta* hoppers. Both Husain & Mathur (1936) and Chauvin (1941) reported far higher proportions of *Schistocerca* hoppers with *gregaria* pattern when crowded with grasshoppers than were obtained in the present experiments.

The tests suggest that the interactions that are involved in the development of social aggregation can be almost fully provided by grasshoppers, but the grasshoppers cannot act as substitutes as far as phase change in colour is concerned.

7. Hoppers Crowded with Woodlice

Since non-gregarious grasshoppers can provide the necessary stimuli for single locusts so to change their behaviour as to aggregate socially when placed with other locusts for the first time, it seemed possible that the behaviour change was a very general kind of habituation. In the following experiments, the locusts were crowded with woodlice. The 360 cc. jars were used and there were three methods of rearing:

(*a*) One locust per jar.

(*b*) One locust per jar plus 20 woodlice (Isopods). The woodlice were mainly *Oniscus asellus* (Linn.) and *Porcellus scaber* (Latr.); a few *Armadillidium vulgare* (Latr.) were also used.

(*c*) One locust with 20 hoppers of the same species and of similar age.

Woodlice normally showed little activity dur-

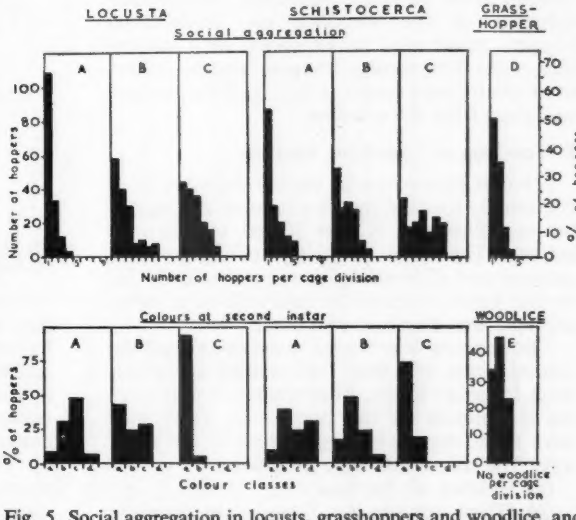

Fig. 5. Social aggregation in locusts, grasshoppers and woodlice, and the colours of locusts reared in various ways in 360 cc. jars from hatching until the time of the test in the second instar. A, one locust per jar; B, one locust and 20 woodlice per jar; C 11 locusts of the same species per jar; D, grasshoppers reared crowded (*Eyprepocnemis*); E, woodlice reared crowded. (For explanation of colour classes see text).

ing the day, but under the conditions of high temperature in the jars they spent a part of the time climbing about the grass stems, provided that the bottoms of the jars were kept clear of rubbish. They were not, however, as active as locusts. When tested by themselves in an aggregation cage, woodlice grouped significantly ($\chi^2 = 52{\cdot}5798$, P=<0·01; Fig. 5, E).

When they were first put with other locusts, the hoppers that had been reared with the woodlice grouped more than the isolated hoppers (Fig. 5, A and B; Table III, v). The hoppers that had been reared crowded with the woodlice did not, however, group as much as the locust hoppers that had been reared with other locusts of the same species (Fig. 5, B and C; Table III, vi), especially in the case of *Schistocerca*. In both species, crowding with woodlice produced only a small shift towards *a*-type colouring.

Although hoppers crowded with woodlice did not aggregate quite so well as those crowded with members of their own species, yet it was clear that woodlice provided stimuli necessary for the change in locust behaviour. Hopper colours on the other hand were comparatively little influenced. The woodlice tended to collect at the bottom of the jars and so had less contact with the locust hoppers than did the grasshopper nymphs in the previous experiment. The smaller influence of the woodlice on *Schistocerca* hoppers might also be explained in a similar way, since *Schistocerca* hoppers tend to collect more often than *Locusta* at the top of the jars and well away from the woodlice.

8. Touching or Exercising Hoppers

A locust placed in a jar containing woodlice is continually touched by the antennae and legs of the woodlice and is thus forced into greater activity. The effect of giving solitary hoppers exercise and of touching them mechanically for several hours, without the intervention of other animals, was therefore examined.

The hoppers were reared in isolation until the second instar and were then treated in various ways for seven hours. After treatment they were fed in isolation for one hour, after which they were tested for social aggregation in the usual way. The treatments were as follows:

(*a*) Isolated all the time.

(*b*) Given exercise for 7 hours. In order to provide exercise, use was made of the fact that locusts climb upwards and will also move towards a light. Each hopper was placed in a cardboard cylinder 2 feet (61 cm.) long which was covered by transparent Polythene at the ends. The cylinders were stood on the floor so that the light entered from the upper ends. The hoppers were kept under observation and as soon as one reached the top, the tube was reversed. There was considerable variation in activity. For the 40 *Locusta*, the mean number of feet climbed in seven hours was 24·8 (range 2-66 feet); for the 40 *Schistocerca*, it was 20·7 (range 2-54 feet).

(*c*) Hoppers crowded in the dark for 7 hours.

(*d*) Hoppers crowded in the light for 7 hours.

(*e*) Hoppers were touched by fine wires during the 7 hours. This was achieved by placing each hopper in a jar that had a lid carrying a spindle. A small wind-vane was fixed to the upper end of the spindle and this rotated a circle of cardboard attached to the lower end just beneath the lid of the jar (Fig. 6). Several fine wires were hung from the circle of cardboard; these moved round and touched the hopper. The wind-vane was driven by air currents from a fan and the rate of turning was very irregular. All hoppers had short rests from being touched during the 7 hours, and they were unable to see each other.

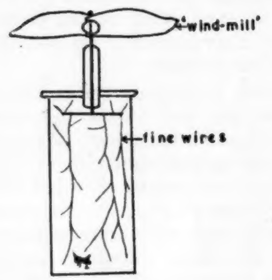

Fig. 6. Diagram of apparatus used for touching hoppers during the experiment illustrated in Fig. 7.

The results are illustrated in Fig. 7. Hoppers that had been given exercise in the tubes behaved in a similar way to those that had been isolated all the time (Fig. 7, A and B; Table IV, i). Hoppers that had been crowded in the dark behaved in a similar way to those that had been crowded in the light (Fig. 7, C and D; Table IV, v). The hoppers that had been crowded for 7 hours grouped significantly more than those that were isolated (*cf.* Fig. 7, A, C and D; Table IV, iv).

The hoppers that had been touched with fine wires showed increased grouping that was almost as marked as that for crowded hoppers (*cf.*

Table IV. Comparing the Numbers of Hoppers Forming Groups in the Experimental Cage after Various Treatments Lasting Seven Hours
(The results for the four tests of each experiment have been added together. The hoppers were reared in isolation prior to treatment and 40 were used for each treatment per species.)

	Reference to fig. 7	Treatments compared	*Locusta*						*Schistocerca*					
			Hoppers in groups of 2 and more			Hoppers in groups of 3 and more			Hoppers in groups of 2 and more			Hoppers in groups of 3 and more		
			Mean difference	t	p	Mean difference	t	p	Mean difference	t	p	Mean difference	t	p
i	A, B	Isolated. Exercised in isolation.	0·8	0·2160	>0·80	1·3	0·8076	>0·40	0·3	0·7220	>0·90	1·3	0·3624	>0·70
ii	A, E	Isolated. Touched by wires.	7·0	2·5350	<0·05	7·5	2·0316	>0·05	10·8	2·8090	<0·05	9·8	1·8190	>0·10
iii	E, D	Touched by wires. Crowded in light.	1·0	0·4491	>0·60	0	—	—	1·5	0·5902	>0·50	4·5	0·6420	>0·50
iv	A, D	Isolated. Crowded in light.	8·0	2·9293	<0·05	7·5	0·3607	<0·01	12·3	3·4445	<0·02	14·3	2·2514	>0·05
v	C, D	Crowded in dark. Crowded in light.	0·3	0·1160	>0·90	0·8	0·3511	>0·70	0·3	0·1644	>0·80	3·8	0·6774	>0·50

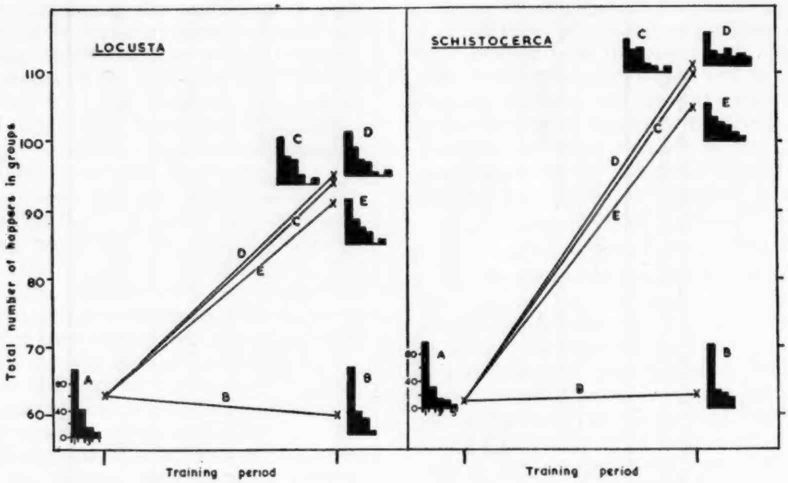

Fig. 7. Illustrating the behaviour of second-instar hoppers reared isolated from hatching until the second-instar and then treated in various ways for seven hours before the test. (Forty hoppers were used for each type of treatment.) A, hoppers isolated; B, hoppers isolated and given exercise for 7 hours; C, hoppers crowded in the dark for 7 hours; D, hoppers crowded in the light for 7 hours; E, hoppers isolated but touched by fine wires for 7 hours.

Fig. 7, D and E; Table IV, ii and iii).

These results suggest that forced activity plays no part in the process of learning to aggregate socially, but that frequent mechanical contact with small objects is a most important factor in it. The learning would appear to be an habituation to being touched by fine processes similar in size to locust legs and antennae. Visual stimuli between hoppers during crowding are apparently not necessary to the learning process.

9. Observations on the Differences in Behaviour Between Isolated Hoppers Placed in a Group for the First Time, and Normally Crowded Hoppers

Detailed observations were made on formerly isolated and crowded hoppers when in groups and when in the presence of other small objects, such as twigs. Locust hoppers continually walk about their cages examining walls, other locusts, pieces of food, etc. When examining objects, isolated and crowded hoppers behave in the same way, lowering the antennae towards the object and sometimes apparently trying to touch it with the palps. The behaviour differs, however, when the hoppers themselves are touched. Isolated hoppers jump or run away; in fact, occasionally a formerly isolated hopper will move away from another that is moving a part of its body rapidly, before they can actually touch. Crowded hoppers do not move away when touched; if one of them is touched by another on the abdomen, it kicks with the hind legs, and if an attempt is made by one to examine another on the head, the latter twirls its antennae. In face-to-face encounters the antennae of two individuals are often moved round each other rapidly without actually touching. If a formerly isolated hopper examines a crowded one, hind-leg kicking or antenna twirling by the crowded locust generally results in the other one jumping or running away. Crowded hoppers do not usually move away when kicked by others and antenna twirling is often mutual among them. In fact, crowded locusts give the impression that mutual examination with the antennae and palps, mutual antenna twirling and hind-leg kicking are positive stimuli which help to keep members of a group together.

If a previously isolated hopper is placed in a small cage with a number of other hoppers it cannot escape continual contacts with them. It gradually becomes less prone to run away when touched and eventually ceases to do so and starts antenna twirling and hind-leg kicking when touched by others. Table V gives the results of a

Table V. Changes in Behaviour Shown by Individual Third-instar Hoppers Reared in Various Ways, when First Placed with a Group of Crowded Hoppers; Two Hoppers of Each Treatment were Observed. (A=violent jump away; B=moved back a few steps; C=sat still; D=sat still and twirled antennae or kicked hind-legs.)

Locust species	Treatment to the time of test from hatching	Number of encounters with other locusts							
		First hour				Fourth hour			
		A	B	C	D	A	B	C	D
Schistocerca	Crowded with other locusts	4	10	18	49		3	8	55
				8	42		6	5	51
,,	One locust plus 20 woodlice per jar	2	8	8	36	1		16	38
			4	4	40		3	5	48
,,	Isolated; touched with fine wires for 7 hours before test	1	7	34	14	3	6	28	36
			7	16	36		2	24	43
,,	Isolated	17	16	9		1	14	28	11
		10	9	8	1	1		38	26
Locusta	Crowded with other locusts	1	8	24	48		1	2	53
		4	2	7	38		2	6	43
,,	One locust plus 20 woodlice per jar	1	4	10	19		3	16	38
		5	5	8	31	2		24	32
,,	Isolated; touched with fine wires for 7 hours before test	3	10	6	24		4	7	38
		1	9	13	19		3	21	29
,,	Isolated	12	18	6	4	2	4	39	17
		10	21	16			8	46	31

few tests in which an attempt was made to measure the strength of the avoiding reactions of previously isolated hoppers in successive encounters with other locusts. Hoppers that had been reared with woodlice or touched repeatedly with fine wires showed far weaker avoiding reactions when first put with other locusts than did the isolated hoppers.

Discussion

Social Aggregation

These experiments and observations suggest that during the earliest stages of gregarisation, when hoppers learn to aggregate socially with one another, there is a simple habituation to being touched. The habituation would appear to involve the tactile sense organs only, since mechanically driven wires provide the necessary stimulation. The habituation is followed by the appearance of two new behaviour patterns that the hoppers show on being touched, namely antenna twirling and hind-leg kicking. Both these activities appear to play a positive role in the group cohesion of crowded hoppers. Further research is required before the nature of them can be understood. Hind-leg kicking may be a much reduced jumping movement. It is interesting that the species of non-gregarious grasshoppers that have so far been investigated do not show this twirling or kicking, even if they have been reared in crowds (unpublished observations on *Eyprepocnemis* and hoppers of *Anacridium* and *Humbe*). It appears that locust hoppers, on the other hand, are born with the ability to learn these reactions under suitable conditions.

A difficult problem that remains to be solved is that of ascertaining the conditions under which hoppers that have lived in isolation in the field will tolerate contacts with other locusts long enough to become habituated to them. Under natural conditions there are no equivalents to the confining walls of a cage. Further research may indicate that isolated hoppers show less violent avoiding reactions during such activities as feeding, or at certain periods during the life cycle, than at other times.

The aggregation cages provide a method of comparing the grouping tendencies of different types of hopper, but the experiments also throw some light on the problem of the behaviour patterns involved in the formation of groups. The analysis of this problem should be divided

into two parts, namely, the attractions of hoppers towards each other over a short distance and the reactions that keep them in groups once they have come close together. It would appear that tactile interactions play an important part in keeping locusts together in groups, but much further work is needed to show if this is the only factor concerned. The coming together of previously crowded hoppers over small distances would appear to involve visual attractions, since the hoppers do not group in the cage in the dark. Whether this visual attraction is for small objects in general or is a specific one for locusts has never been tested.

In isolated hoppers, learning to aggregate appears to be largely an habituation to being touched. The fact that isolated hoppers touched by fine wires grouped when first put together suggests that such hoppers possess the behaviour patterns necessary for attraction towards one another over small distances, but lack those reactions that keep them with other locusts once they have met.

Colour Changes

Changes in hopper colour come later in the process of gregarisation, so it is hardly surprising that they depend on different mutual stimulation to social aggregation. In fact, the two processes are very different. While learning to aggregate socially appears to be mainly an habituation to being touched, the colour change depends on the total of the mutual stimulation from all sources. In contrast to the results of past workers (Husain & Mathur, 1936; Chauvin, 1941) it was found impossible to obtain fully gregarious coloration in all hoppers reared crowded with grasshoppers, and the full change to phase *gregaria* coloration appeared to require crowding with locusts of the same species. In careful experiments in which he tried to separate visual, olfactory, tactile and auditory stimuli between hoppers during rearing, Nickerson (1954) found that all these stimuli could be proved to be of importance in the colour change. There was some evidence of interaction between the stimuli, and it seemed possible that those from the various sense organs were, to a certain extent, interchangeable. It may be that it is the total stimulation of all kinds from other locusts that is of importance, rather than stimulation through particular sense organs (*cf.* Ellis & Hoyle, 1954, on marching).

Differences Between the Two Locust Species

On the whole, the amount of grouping shown by isolated and crowded hoppers was higher in *Schistocerca* than in *Locusta*. This may mean that social aggregation is better developed in *Schistocerca*. For both species, the difference in the number grouped was similar (mean difference about 10) when isolated hoppers were compared with those reared crowded at ten per jar. When isolated hoppers were compared with hoppers reared crowded in much larger numbers in cages, the differences may have been greater in *Locusta* than in *Schistocerca*. (For *Locusta*, the mean difference was 16·3, and for *Schistocerca* 11·5.)

Crowding single locusts with grasshoppers increased grouping by similar amounts in both species; in comparison with isolated hoppers, the mean difference was about 10. Woodlice, however, influenced *Locusta* more than *Schistocerca* (the mean number grouped being 13·0 for *Locusta* and 8·5 for *Schistocerca*). The possibility that *Locusta* hoppers had more contacts with the woodlice than had the *Schistocerca* hoppers has already been mentioned. The experiment illustrated in Fig. 7 suggests that learning to aggregate socially was a more rapid process in *Schistocerca* than in *Locusta*.

The experiments with mirrored jars and rearing single hoppers in transparent boxes placed inside a cage full of other hoppers suggest that a combination of visual, olfactory and auditory stimuli from other locusts improved social aggregation in *Locusta* only. (Comparing isolated hoppers and those in mirrored jars, the mean difference for *Locusta* was 5·0, and for *Schistocerca* 2·8. Comparing hoppers isolated in boxes and those in boxes in a crowd, the mean difference for *Locusta* was 9·0 and for *Schistocerca* 2·3.) Only further work can show if this is a fundamental difference between the two species.

Changes in colour for the two species are very difficult to compare since the colour classes have no meaning in quantitative terms. There was, however, an indication that *Schistocerca* hoppers were more sensitive to gregarising factors, so far as the change in colour was concerned, than the *Locusta* hoppers. This was so when single hoppers were crowded with grasshoppers and when single hoppers were reared in boxes placed in a cage full of hoppers. In other kinds of experiment on hopper colour changes, Chauvin (1941) and Hunter-Jones (1958) showed a greater sensitiveness in *Schistocerca* than in *Locusta*.

Summary

1. When locusts swarm, the hoppers (nymphs)

live together in bands that depend on the individuals being attracted towards one another (phase *gregaria*, obtained in the laboratory by rearing hoppers together in crowds). They are then said to aggregate socially. This behaviour pattern can be measured in the laboratory in a cage that provides a physically uniform environment. In non-swarming periods, the scattered hoppers (phase *solitaria*, obtained in the laboratory by rearing hoppers in isolation) are not attracted towards one another when first confined together. If hoppers that have been reared in isolation are forcibly crowded together they learn to aggregate socially within a few hours. The types of stimuli between hoppers that are of importance during the process of learning to aggregate socially were studied in the two locust species *Locust migratoria migratorioides* (R. & F.) and *Schistocerca gregaria* (Forsk.).

2. Single hoppers reared with a crowd of non-gregarious grasshoppers or woodlice (Isopods) aggregated socially when first placed together.

3. By rearing single hoppers in transparent boxes placed in a cage full of other hoppers, direct tactile contact with other hoppers was eliminated, but visual, auditory and olfactory stimuli were received from the others. In such box-reared hoppers, social aggregation was increased a little in *Locusta*, but not at all in *Schistocerca*.

4. Previously isolated hoppers showed increased grouping after being crowded with other hoppers for only seven hours. Crowding in the dark produced similar results to crowding in the light. Social aggregation was also increased in hoppers that were reared isolated but touched with fine wires for a seven-hour training period before being tested; they grouped almost as well as hoppers that had been crowded with other locusts.

5. The behaviour patterns shown by crowded and by previously isolated hoppers when they first meet others are described. Both types of hopper examined objects, including other locusts, with the antennae and palps, but they differed in behaviour when they were themselves touched. Previously isolated hoppers moved away; crowded hoppers remained where they were and kicked with the hind legs or twirled the antennae. During the process of learning to aggregate socially, previously isolated hoppers appear first to become habituated to being touched. This is followed, after further contacts, by hind-leg kicking and antenna twirling, and these probably play a positive role in keeping the hoppers together in groups. The complete learning process can be brought about by touching isolated hoppers repeatedly with fine wires before they are put with other locusts.

6. In contrast to locusts, grasshoppers do not aggregate socially even when reared in crowds.

7. Records of colour changes were kept during the experiments. Phase *gregaria* hoppers are typically black and orange or yellow, whilst phase *solitaria* hoppers are mainly green or fawn. The various treatments suggested that phase *gregaria* colouring depended on a complex of stimuli between hoppers, through the auditory, visual, olfactory and tactile sense organs.

8. On the whole, the two species of locust gave similar results. The process of learning to aggregate socially was a little more rapid in *Schistocerca* than in *Locusta*.

Acknowledgments

The Anti-Locust Research Centre provided funds for this work. Thanks are due to Professor Varley for laboratory facilities at the Hope Department of Entomology, Oxford; to Mr. E. Taylor of the Hope Department for identifying the woodlice; and to Mrs. J. Wallace and Mrs. D. Wort for assistance with some of the experiments and the former also for assisting in the design and manufacture of the "touching machines."

REFERENCES

Chapman, R. F. (1959). Field observations on the behaviour of hoppers of the Red Locust (*Nomadacris septemfasciata* Serville). *Anti-Locust Bull.*, No. **33**, 51 pp.

Chauvin, R. (1941). Contribution à l'étude physiologique du criquet pèlerin et du déterminisme des phénomènes grégaires. *Ann. Soc. ent. Fr.*, **110**, 133-272.

Ellis, P. E. (1951). The marching behaviour of hoppers of the African Migratory Locust (*Locusta migratoria migratorioides* R. & F.) in the laboratory. *Anti-Locust Bull.*, No. **7**, 48 pp.

Ellis, P. E. (1953). Social aggregation and gregarious behaviour in hoppers of *Locusta migratoria migratorioides* (R. & F.). *Behaviour*, **5**, 225-260.

Ellis, P. E. (1956). Differences in social aggregation in two species of locust. *Nature* (*Lond.*), **178**, 1007.

Ellis, P. E. & Ashall, C. (1957). Field studies on diurnal behaviour, movement and aggregation in the Desert Locust (*Schistocerca gregaria* Forskål). *Anti-Locust Bull.*, No. **25**, 94 pp.

Ellis, P. E. & Hoyle, G. (1954). A physiological interpretation of the marching of hoppers of the African Migratory Locust (*Locusta migratoria migratorioides* R. & F.). *J. exp. Biol.*, **31**, 271-279.

Faure, J. C. (1932). The phases of locusts in South Africa. *Bull. ent. Res.*, **23**, 293-405.

Hunter-Jones, P. (1958). Laboratory studies on the inheritance of phase characters in locusts. *Anti-Locust Bull.*, No. **29**, 32 pp.

Husain, M. A. & Mathur, C. B. (1936). Studies on *Schistocerca gregaria* Forsk. V. Pigmentation and physical exertion. *Indian J. agric. Sci.*, **6**, 591-623.

Johnston, H. B. & Buxton, D. R. (1949). Field observations on locusts in eastern Africa. *Anti-Locust Bull.*, No. **5**, 74 pp.

Kennedy, J. S. (1939). The behaviour of the Desert Locust (*Schistocerca gregaria* (Forsk.)) (Orthopt.) in an outbreak centre. *Trans. roy. ent. Soc. Lond.*, **89**, 385-542.

Kennedy, J. S. (1956). Phase transformation in locust biology. *Biol. Rev.*, **31**, 349-370.

Maxwell-Darling, R. C. (1936). The outbreak centres of *Schistocerca gregaria*, Forsk., on the Red Sea coast of the Sudan. *Bull. ent. Res.*, **27**, 37-66.

Nickerson, B. (1954). Pigmentation of Desert Locust hoppers (*Schistocerca gregaria* Forsk.) in relation to phase coloration. *Ph.D. Thesis, University of London.*

Stower, W. J. (1959). The colour patterns of hoppers of the Desert Locust (*Schistocerca gregaria* Forskål). *Anti-Locust Bull.*, No. **32**, 75 pp.

Uvarov, B. P. (1921). A revision of the genus *Locusta* L. (=*Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts. *Bull. ent. Res.*, **12**, 135-163.

Uvarov, B. P. (1928). *Locusts and grasshoppers*. London: Imperial Bureau of Entomology.

Uvarov, B. P. (1937). Biological and ecological basis of locust phases and their practical application. *4th Int. Locust Conf.*, Cairo 1936, Appendix 7, 16 pp.

Volkonsky, M. (1942). Observations sur le comportement du criquet pèlerin (*Schistocerca gregaria* Forsk.) dans le Sahara algéro-nigérien. *Arch. Inst. Pasteur Algér.*, **20**, 236-248.

Zolotarevsky, B. N. (1930). Le criquet migrateur (*Locusta migratoria capito* Sauss.) à Madagascar. *Ann. Épiphyt.*, **15** (1929), 185-236.

Zolotarevsky, B. N. (1933). Contribution à l'étude biologique du criquet migrateur (*Locusta migratoria capito* Sauss.) dans ses foyers permanents. *Ann. Épiphyt.*, **19**, 47-142.

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PLATE I

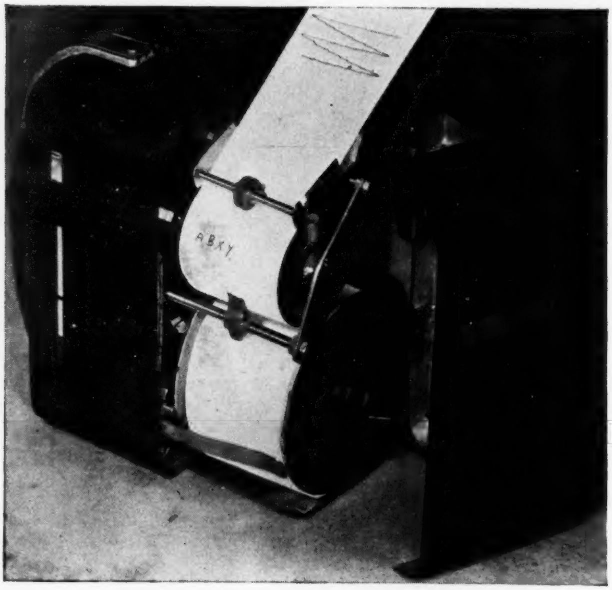

Fig. 1. The complete instrument, with the lid open.

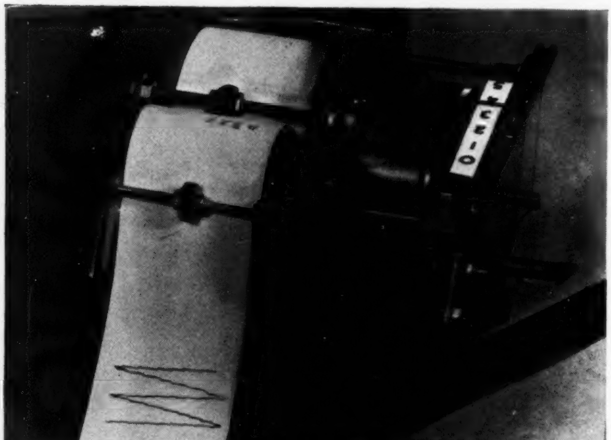

Fig. 2. The instrument removed from its case. The clockwork is in the foreground, with the scale and the stop/go switch above, and the winding key on the side.

AN AID TO FIELD OBSERVATION

By J. R. TROTTER

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Introduction

When an observer makes notes during a long spell of observation, repeated consultation of a clock and writing down the time, besides making the work more arduous, distract attention from the main task. The machine described here was made to provide a timed record of observations of animal behaviour in the field, without the need for consulting a clock. Other work for which it would be useful includes traffic observation and work study.

The requirements of the machine were portability, independence of external power, and temporal stability.

General Description

A strip of paper is unwound from a roll and passed in small steps behind a slit. The steps are of constant size and recur at a constant interval. Notes of observations may be written on the exposed paper, and distances on the paper indicate the durations of and the intervals between the events described. For standardized events a position code may be used, the slit being marked off into a number of channels requiring only signs for start and stop. When a pencil is drawn along the side of the slit a stepped line is produced. The number of steps indicates the time spent in drawing the line, in terms of the constant interval. This procedure is useful when the observed events last only a few seconds.

The machine is housed in a steel case, with a lid allowing access for loading the roll and threading the paper over the driving roller. On the top of the case are the writing slit, a stop/go switch, and a scale indicating running time left. A winding key is stored inside the case, and the used paper comes out of a gap in the case.

Design

It was established that a pull of 4 oz. on the paper is sufficient to overcome any normal load imposed by a pencil in writing. A design figure of 8 oz. allows for incidental losses. With a paper speed of 1 mm./sec. the power requirement is about 70 in. lb/hr. A gramophone spring (14′ × 1″ × 0·025″ in a 2¾″ shell) used over the range of 1/3 to 2/3 of full wind, gives a running time of 5 hr. without excessive variation of torque.

The train of gears from the winder to the escapement of an ordinary alarm clock, without the mainspring, is used. The maximum winding torque, before the balance wheel is over-driven, is about 4 lb. in., and the winder makes 1/6 rev./hr. With a design figure of 3 lb. in. the power is about 3 in. lb./hr. Thus the clock cannot control the required power of 70 in. lb./hr. If it were put in the gear train so as to give the correct paper speed, the force on the paper would be too small. If it were arranged to give the correct driving force, the paper speed would be too small. The clock's power must be increased by a factor of 70/3, by increasing its torque and/or its speed, and this is done as follows.

When all but one of the teeth are removed from the wheel of the lever escapement, it makes a whole revolution during one tick-tock, instead of advancing only one tooth. The alarm clock wheel had 15 teeth, allowing a 15-fold increase in speed, made up of a 3-fold increase of movement on the tick and 12-fold increase on the tock. Thus there are actually two sizes of step, but the smaller is not perceptible on the paper.

When part of the outer edge of the remaining tooth, driving the pin on the lever, is removed, a larger force may be used. Since contact is maintained for a shorter time the maximum safe impulse to the balance wheel is not exceeded. An increase of 1½ times is easily obtained. With the 15-fold increase in speed, it brings the power to the required value—$15 \times 1\frac{1}{2} \bumpeq 70/3$.

The main components, clock, spring and gear wheels can be bought for a few pounds.

Specification

Overall dimensions:	6½ × 5¾ × 3¾ in.
Weight:	5½ lb.
Running time:	5 hr.
Paper reserve with 3½ dia. roll:	20 hr.
Paper width:	2 in.
Slit dimensions:	1⅞ × ½ in.
Paper speed:	56 mm/min.
Speed stability:	As the alarm clock's.
Time unit for each step:	0·6 sec.

Accepted Dec., 1956—*publication unavoidably delayed.*

PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

A Joint Meeting with the Experimental Psychology Group was held at Cambridge on 26th and 27th March, 1958. The theme of the discussion was "Discriminating Mechanisms" and the following papers were read.

STEREOSCOPIC VISION: BINOCULAR TEMPORAL SUMMATION

By R. EFRON
Neurological Research Unit, National Hospital, London

Simultaneous viewing by both eyes is not a necessary condition for stereoscopic vision. The illusion of depth produced by a Wheatstone-Brewster stereoscope will still occur if each eye is exposed separately to the visual scene. If an isolated exposure is administered to each eye, the interval between exposures cannot exceed ten milliseconds for stereoscopy to be retained. On the other hand, if a long train of alternating right and left eye exposures is produced, the interval between any right and left eye exposures (couplets) may be prolonged to one hundred milliseconds.

A brief exposure of one eye to the stimulus containing only "parallactic" information appears to establish a central excitatory state which is still sufficiently strong after ten milliseconds for interaction to occur with the stimulus arriving from the other eye. If the delay is greater than this, interaction (stereoscopy) will not result unless additional stimuli are administered. This repetition of subliminal stimuli to produce the same end result (which in this case is a complex sensory illusion) is, by definition, temporal summation.

As the maximum delay between exposure of right and left eye with a series of subliminal stimuli is one hundred milliseconds, a ten-fold increase can thus be secured in the duration of the effective central excitatory state. Further factors which influence the duration of maximum delay between exposures to the two eyes are (*a*) the brightness of the scene and (*b*) the duration of the exposure,

TACTILE LOCALISATION

By C. R. E. HALNAN and G. H. WRIGHT
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In a routine class-experiment in which the *toes* were used as test-sites, we noticed that some subjects made fewer errors if they were allowed to look at their toes immediately after the withdrawel of the stimulus-object. This effect was not due to such cues as pitting or blanching at the spot touched. We decided to test it rigorously, for both fingers and toes, in a series of sixteen young adults of good intelligence and normal health. Observations made in this series led to further experiments, including a series designed to test the importance of *movement* as an aid to tactile localisation. Our conclusions are based in part on an analysis of the objective results (numbers and types of errors) but also, to a large extent, upon the comments and opinions of the participants, offered both spontanesously and in answer to questions.

At some sites the subjects' responses were usually quick and accurate, and neither subject nor experimenter could make any observations of value as to the processes involved. At other sites there was delay, and the subjects were often able to give an account of their sensations, dilemmas and methods of deciding. The importance of visual factor was established, and likewise the importance of movement. Among other factors shown to be of importance were tactile after-effects, sensations of touch which spread so as to involve the whole of a web between two

fingers or toes, pressure-sensations, and thermal sensations. We were also given some insight into the conceptual processes involved.

We arrived at some conclusions about the way in which the ability to localise a touch may be acquired, and also about some ways in which one might expect this ability to be affected by cerebral lesions.

SOME EFFECTS OF RESERPINE ON BEHAVIOUR IN THE RAT

By P. H. GLOW

M.R.C. Unit, Department of Psychology, University College, London

Experiments reported so far with the drug reserpine have been confined to the use of extremely small doses, i.e. doses which weight for weight are sub-clinical. More substantial doses produce a behaviour failure akin to a catatonic-like breakdown. Experiments will be described which demonstrate the dose levels and time factors involved in this breakdown and an attempt will be made to associate these behavioural changes with change cerebral biochemistry. Further experiments will be described which demonstrate that the concurrent extrapyramidal overactivity and fall in deep body temperature are not themselves instrumental in the behaviour changes observed. The reserpine condition can be quickly reversed by the injection of a new sympathomimetic drug methyl phenidate.

These experiments are particularly of interest when considered in relation to the action of the halliconogenic drug, lysergic acid diethylamide. Experiments will be described which associate the residual biochemical disturbance induced by reserpine with the action of LSD-25.

THE ANALYSIS OF OPTOMOTORIC REACTIONS IN INSECTS AND CRUSTACEA

By B. HASSENSTEIN

Forschungsgruppe Kybernetik des Max-Planck-Instituts für Biologie, Tübingen

Vision of movement in all animals and men involves a physiological interaction between adjacent visual units. This interaction was shown to be a process of cross-correlation in the beetle *Chlorophanus viridis*. The eyes of this insect are composed of facets (ommatidia) which act as visual units in the process of perception of movement. The visual fields of adjacent ommatidia do not overlap. One point-like visual stimulus is received only by one ommatidium and not by its neighbours. The anatomical angle between the axis of two adjacent facets is 6·8°. Many animals, including *Chlorophanus*, react to the perception of movement in their visual field by optomotor reactions. They follow the movement which they perceive by active turning reactions of their head or their body and so reduce the movement stimulus which they receive by their eyes. This may be described in terms of a feed-back loop.

The direction and strength of the optomotor response has been used as an indicator of the perception processes in the nervous parts of the eyes of the experimental animal. In the experiments the feed-back loop of the reaction has been cut off by fixing the animal so that its optomotor reactions could be observed by the experimenter but did not influence the position of the animal itself in relation to its optical environment. The experimental procedure (Y-maze-globe method) is shown in Fig. 1.

Successions of practically point-like light stimuli were delivered to the eye of the experimental animal. If A, B, C, D . . . . are adjacent ommatidia in a horizontal row and if the sign "+" is given to a stimulus which consists of an illumination change from darker to lighter the formula $+A(t_1)+B(t_2)$ describes a succession of two stimuli in adjacent ommatidia. The same succession may be written also $F^{++}_{AB}(t_1, t_2)$. The reaction of the animal to F^{++}_{AB} may be symbolised by R^{++}_{AB}.

Results

1. The basic stimulus situation which is able to make a contribution to an optomotor response consists of two successive stimuli in adjacent ommatidia. All optomotor responses to

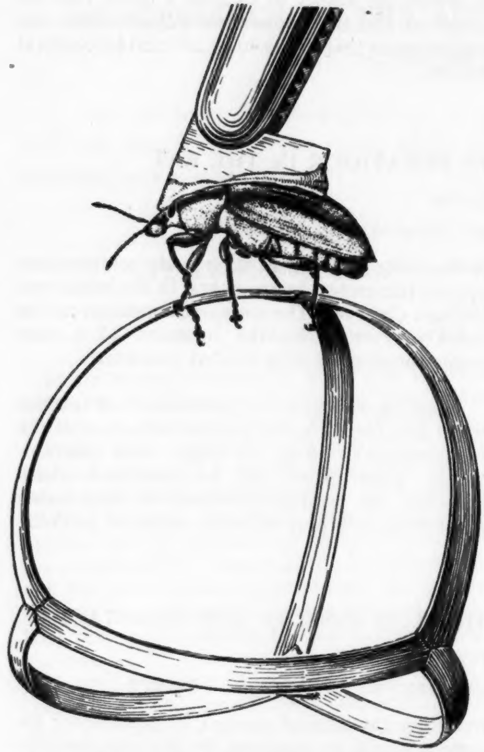

Fig. 1. Y-maze globe method. The beetle's back is glued to a piece of cardboard which is held by a clip; the clip is fixed to a stand, so the beetle is freely suspended in the air. The beetle is given the "Y-maze-globe" which he carries of his own free will. The Y-maze-globe is made of 6 straw pieces which join in four points to form Y-like junctions. When the beetle starts walking he remains fixed, but the Y-maze-globe performs the negative of the movements the beetle would perform if he were walking freely. After a few steps the beetle reaches a Y-junction, or better, a Y-junction reaches him, and the beetle has to choose right or left. After passing the junction the animal is in the same position as before. After the next few steps it has to choose again, and so on. For the beetle the Y-maze-globe is an infinite Galton probability apparatus. In a given optical stimulus situation the ratio of choices of the right and the left pathway has been proved to be a sensitive quantitative measure of optically induced (optomotor) turning tendencies. Beetles which were suspended in the centre of a very slowly rotating stripe cylinder showed clear reactions to angular movements of 0.02°/sec.; this is a quarter of the angular velocity of the minute hand of the clock. Drawing by E. Freiberg, after a photograph.

complex stimulus situations can be shown to be built up from these basic functional units.

2. In producing optomotor responses each ommatidium can only cooperate with its immediate neighbour or with the next but one. There is no physiological interaction between ommatidia which are separated by more than one unstimulated ommatidium.

3. The maximum reaction is given in the case of a time interval between two stimuli of about 150 msec. The strength of reaction decreases with both greater and smaller time intervals. The maximum time interval which was shown experimentally to release a reaction was about 10 seconds. One must conclude that the first stimulus has an after-effect of 10 seconds or more which later disappears. The real physiological interaction takes place between the after-effect of one stimulus and the effect of a following one. The first stimulus of a succession of two stimuli is modified by a transmitting element of large inertia.

4. $R^{+++}_{ABC} = R^{++}_{AB} + R^{++}_{BC} + R^{++}_{AC}$
i.e. the cooperation between the functional units (see 1 and 2) is summative.

5. $R^{++}_{BA} — R^{++}_{AB}$
i.e. reversed time sequences of stimuli release reverse optomotor responses.

6. $R^{--}_{AB} = +R^{++}_{AB}$
i.e. successions of negative illumination changes (changes from lighter to darker) release the same reaction as successions of positive ones.

7. ${}^{+-}_{AB}R = R^{-+}_{AB} = —R^{++}_{AB}$
i.e. successions which consist of one "+" and one "—" stimulus release negative (reverse) optomotor responses.

8. As it has been known for a long time a cylinder of *grey* stripes on white background releases weaker optomotor reactions than a cylinder of *black* stripes on the same background which rotates with the same angular velocity, i.e. the strength of optomotor reaction of insects does not only depend on the velocity of the moving pattern but also on the contrast of its constituents. In an experiment I kept the time intervals constant and varied the contrasts of the pattern, that is the individual stimulus intensities. The result of this experiment was that the strength of reaction is a *quadratic* function of the stimulus intensities.

The experimental results 7 and 8 may be described together as follows: the direction and intensity of the optomotor response reflect the multiplication result of signs and intensities of two interacting individual stimuli. There must be a physiological mechanism which causes that the sensory input and the motor output are

linked by a process which works according to the formula of multiplication.

9. If a regular or irregular pattern of shades from white through black passes two light sensitive inputs, and if the generated messages—after being modified by special transmitting elements (see para. 3)—are multiplied with each other the output of the system changes with different velocities of the pattern. This has been worked out mathematically by Reichardt (1957).

The quantitative result has been tested in the beetle *Chlorophanus* by measuring the strength of its optomotor response to different speeds of moving patterns. The result matched the theoretical curves very well. One must conclude that the multiplication process (see para. 8) represents the nervous interaction mechanism which provides the CNS of the beetle with the information about the direction and strength of visual movements.

We get a better understanding of this mechanism if we take in mind that multiplication is the essential procedure in getting a correlation coefficient i.e. a measure of similarity between different successions of dates which have to be compared. The multiplication mechanisms in the eye cf. the CNS of the beetle can be taken as a set of systems which measure the degree of correlation between the messages which are received by adjacent ommatidia. The correlation between the after-effect of the message in one ommatidium and the effect of the corresponding stimulus in the adjacent ommatidium will be the better the shorter the time interval is between the two events, since the strength of the after-effect diminishes in time. Therefore correlation in this system is a measure of velocity. The principle of measuring speed by a correlation process can be used in "ground speed analyser" systems of aircraft.

REFERENCES

Hassenstein, B. (1951). *Z. vergl. Physiol.*, **33.**
Hassenstein, B. (1958a). *Z. vergl. Physiol.*, **40.**
Hassenstein, B. (1958b). *Z. Natur.-Forsch.*, **13b.**
Hassenstein, B. & Reichardt, W. (1953). *Z. Natur.-Forsch.*, **8b.**
Hassenstein, B. & Reichardt, W. (1956). *Z. Natur.-Forsch.*, **11b.**
Reichardt, W. (1957). *Z. Natur.-Forsch.*, **12b.**

A TEST OF THEORY OF SHAPE DISCRIMINATION IN *Octopus vulgaris* LAMARK

By N. S. SUTHERLAND

Institute of Experimental Psychology, University of Oxford

A hypothetical mechanism for the visual discrimination of shape in *Octopus vulgaris* Lamark is described. The essence of the mechanism is that in the octopus's nervous system shapes are analysed into their vertical and horizontal projections. Any pair of shapes which have the same horizontal and vertical projections should therefore be indiscriminable. Experiments are described in which octopuses were given discrimination training on different pairs of shapes, matched for their complexity: some of the pairs had the same horizontal and vertical projections as one another, others differed in their horizontal and vertical projections. It was found that although the former pairs were sometimes discriminable, they were discriminated much less readily than the latter pairs. It was further found that the discriminability of mirror images seems to depend upon whether or not they have the same horizontal and vertical projections as one another. Although these results seem to give some support for the theory, the fact that some shapes not differing in their horizontal and vertical projections are discriminable means that the theory is in need of some modification or addition. A sudsidiary finding, not accounted for by the theory, is that octopuses have a preference at the time of entering the laboratory for shapes moving in the direction of their long axis or in the direction of their points.

TACTILE DISCRIMINATION IN Octopus

By M. J. WELLS

By training blinded octopuses to discriminate between the members of pairs of objects that differ in only one way at a time we can find out what features of objects touched are recognisable to them. It is possible to demonstrate a direct relationship between the difference in texture and the difficulty that octopuses have in distinguishing between any two objects, irrespective

of the pattern or orientation of surface irregularities. From this and from the failure of octopuses to learn to discriminate between objects, such as lamellibranch shells of various species, having different shapes but similar surface textures, it can be argued that the animals are unable to distinguish the shape of objects that they touch.

This inability seems to be a consequence of the extreme flexibility of the arms of *Octopus*. Animals, such as ourselves, which can distinguish the shape of objects by touch presumably do so by integrating information from their tactile sensory endings with information about the relative position of these endings derived from sense organs located in their muscles and joints. The complexity of nervous system necessary to do this depends upon the number of successive joints and the degree of freedom that each allows.

Octopus has no joints, so that the number of possible bending places and positions of its eight arms and two thousand-odd suckers is for all practical purposes infinite. It is most improbable that the animal has a sensory apparatus of the complexity necessary to define the relative position of its armtips, let alone of the suckers, at all accurately. Discrimination experiments show that even if such a system exists, *Octopus* is unable to integrate the information derived from it with that from its surface tactile sense organs, and so cannot gain additional information about objects touched by comparing impulse patterns from neighbouring groups of sense organs.

Consideration of the structure of the tactile sensory system in the light of its known properties suggests that *Octopus* learns to recognise objects by the characteristic frequencies that their surface textures produce in the nerves coming from the arms, and that the integrative work done by the brain is relatively simple.

The extent to which the structures associated with tactile learning are localised in the nervous system can be traced by comparing the performance of animals in training experiments made before and after surgical interference with their brains. Removal of the optic lobes, together comprising somewhat more than half of the total mass of the brain, has no effect upon *Octopus's* ability to make simple tactile discriminations.

Damage to the vertical lobe—a considerably smaller volume of tissue—has effects that may be broadly described as decreasing the efficiency of the learning process; the animal requires more trials to attain a given standard of response. Removal of further parts of the supraoesophageal brain mass has no appreciable effect upon tactile discrimination until the lesion includes parts of the inferior frontal-subfrontal lobe system. Extensive damage to either of these small lobes destroys *Octopus's* ability to learn to discriminate between objects by touch, although having no effect on the execution of movements of acceptance or rejection.

We can, in fact, take the matter further than this and show that there are functional divisions within the inferior frontal-subfrontal system. By training the animal to reject an object presented always to the same arm, and then changing the arm, we can demonstrate that the effect of experience of one arm does not at once spread to determine the reactions of the rest; we have, literally, a situation where "the right hand does not know what the left is doing", and it seems wholly probable that this implies the existence of neurone fields representing individual arms within the lobes dealing with tactile integration.

Since removal of the inferior frontal-subfrontal system does not affect *Octopus's* visual learning it is concluded that these parts are exclusively concerned with the integration of surface tactile information. As this integration appears to be limited to frequency discrimination, there is reason to believe that the inferior frontal-subfrontal octopus preparation will prove to be unusually favourable material for the study of learning processes and the structures associated with them.

SOCIAL INTERACTIONS IN DISCRIMINATION LEARNING

By P. KLOPFER

Ornithological Field Station, Madingley; Department of Zoology, Cambridge

A full understanding of the ontogeny of species-specific food preferences requires a knowledge of the effects of social interactions on discrimination learning. In this study, learning rates and processes were compared in paired and single birds.

The term "empathic learning" has been proposed as a rubric covering all forms of motor mimicry. Processes involved may include secondary conditioning, social facilitation, local enhancement, or visual imitation. There is evidence supporting the operation of all these in avian behaviour, except the last.

Birds (greenfinches, *Chloris chloris*) were trained to feed from one of two patterns and to avoid the other, with whole and aspirin-filled sunflower seeds serving as positive and negative reinforcement. Single birds learned the discrimination rapidly, as did birds which had been allowed to observe a previously trained bird performing. Birds which were being trained in the presence of an untrained partner, however, required much longer. When birds of this last group were permitted to observe the training sequence of their untrained partners, their performances repeatedly fluctuated to a random or nondiscriminatory level. The partners, in turn, also fluctuated between random and nonrandom levels. Behavioural data preclude the operation of local enhancement or social facilitation. The results are interpreted to mean that, under the conditions of the experiments, a feeding response can be established more readily than an avoidance response, apparently as the result of secondary conditioning (the unconditioned stimulus being the sight of another bird feeding). The suggestion is made that birds which show this type of learning pattern in nature will prove to be conservative in their feeding habits when compared with opportunistic species (e.g. *Parus* sp.) whose learned avoidance responses should be more stable.

SOME PROBLEMS IN LOCALISATION OF HORMONAL ACTION ON THE C.N.S.

By R. WARREN

No précis of this paper was available at the time of going to press.

At an Ordinary Meeting on 23rd September, 1958, held in the Department of Psychology, Birkbeck College, London, the following papers were read. The President was in the Chair.

REFLEX RESPONSES IN FLYING INSECTS

By L. GOODMAN

Queen Mary College, University of London

The initiation of flight, its regulation, maintenance and cessation all depend upon the interaction of a large number of reflex reactions. Some results of an examination, at present in progress, of the part played by visual stimuli in the maintenance and regulation of flight and in the orientation of the flying insect in its environment were described, with special reference to the behaviour of the desert locust, *Schistocerca gregaria.*

The relationship between the light intensity at which the insect was flown and the flight posture, readiness to fly and duration of flight was first examined. The locusts were attached by the thorax to a light weight, rigid pendulum capable of movement only in the vertical plane through the long axis of the body. They were attached to the pendulum by two rings which allowed freedom to chose their angle of attack but no movement in the rolling or yawing planes. The mounted insect was placed in front of a small wind tunnel and was enclosed on five sides by a wooden box. The light intensity could be set at any desired value, and it was shown that the angle of pitch, the readiness to fly and the duration of flight recorded over a timed period were not affected to any marked degree by this factor in *Schistocerca gregaria* or in *Lucilia sericata* and *Muscina stabulans*, the two flies tested. The light intensity did have a marked effect on night-flying moths however, the wing beat frequency being higher and duration of flight longer at low intensities.

Sudden changes in the surrounding intensity

produce changes in the wing beat frequency of locusts which persist for a few seconds. An increase of intensity produces a decrease in the wing beat frequency and a decrease of intensity produces an increase in frequency. The temporary increase in flight speed and the consequent forward movement were measured directly and used to determine the ability of the locust to detect a decrease of light intensity. The ocelli did not normally mediate the response, having a very high threshold, but the ability of the compound eyes to detect changes of light intensity was considerably diminished if the ocelli were occluded. In contrast, the wing beat frequency of many other insects, for example flies and bees, decreased when the light intensity was decreased the insect lowering the legs preparatory to landing.

The part played by light in maintaining stability in the rolling plane in the locust has also been examined. Mittelstaedt (1950, *Z. vergl. Physiol.*, **32**) showed that the dragonfly, *Anax imperator*, orientates itself when flying so that the greater light intensity falls on the dorsal ommatidia, the head moving in response to the light stimulus and the body being orientated in relation to the head. Movement of the head in relation to the body is detected by four groups of prothoracic hairs. Locusts were mounted on a support which gave them freedom to rotate and remain stable in any position about their longitudinal axis. They were placed in an open ended box, facing a wind tunnel, with the head at the intersection of four horizontal beams of light, one beam being directed from the centre of each wall. The head in locusts does not act as an organ of balance since locusts flown in complete darkness were unstable in the rolling plane, revolving slowly round their longitudinal axis. When any one of the light beams was switched on the locust turned about its longitudinal axis until the light fell upon the dorsal ommatidia and continued to fly in this position as long as the light was on. Some light in the sky, even if only equivalent to starlight, appears to be necessary for stable flight in locusts. A hair plate has been found at the tip of each of the first cervical sclerites of locusts at the point where it forms a ball and socket joint with the post occipital condyle. (A detailed description of these hair plates is to be published.) Movement of the head relative to the body causes deflection of these hairs and also of the fringe of prothoracic hairs which extends forwards as far as the head. If either the prothoracic hairs or the hair plates were removed the locust had difficulty in remaining orientated to the light and if both were removed then continued orientation to the light was impossible. The body could not be orientated in relation to the head and its momentum carried the locust on beyond the light so that a slow spinning resulted. The presence of the intact hair plates and prothoracic hairs is therefore essential for the dorsal light reaction to operate in maintaining stable flight in the rolling plane.

SHAKING OF HONEYBEE QUEENS IN RELATION TO SWARMING

By DELIA M. ALLEN

Bee Research Department, Marischal College, Aberdeen

The process known as "shaking" is quite characteristic and is carried out by an apparently fairly small number of workers in the honeybee colony. A shaker moves from one bee to another resting its legs or head against each one and rapidly vibrating its abdomen in a vertical direction for one or two seconds. It then moves on to shake another bee in its course. The most noticeable point about shaking, and one which makes it seem surprising that it has not been more widely reported, is its appearance of being a very methodical activity, with the shaker usually moving over the combs for relatively long periods and shaking bees with considerable regularity.

Both the queens and the workers may be shaken, as a few writers have reported, but the significance of shaking has remained obscure, although it has been suggested that it might have a connection with mobilisation for flight.

Frequent observations showed that the queens were not shaken throughout the year. Two colonies were studied in two different years, and observations were begun in early May in the first case and in April in the second, being terminated when the prime swarms left, but shaking was not

observed until after the first drone eggs were laid and the first queen cups were built. As swarm preparations continued, however, the queen was shaken progressively more frequently and a peak was reached on the day the swarm left. In neither colony were observations made on the new queens before they mated, but it was found that once the young queen of the second colony had commenced laying eggs the frequency with which she was shaken fell very rapidly.

In contrast to the queen, the results made it plain that the workers may be shaken at any season. Records from the period prior to swarm preparations showed that a number of marked workers which had been seen to shake other workers before joining the circle of the queen's attendants left again without shaking her, thus indicating that the absence of shaking of the queen at this time was not due to a lack of potential shakers in her neighbourhood.

The number of the queen's shakers rose as their age increased and very few bees under 10 days old were observed to shake her.

The present observations did not cover the time between the emergence and mating of the young queen, but Hammann (1957) has made a series of observations during this part of the life cycle. She found that the virgins were shaken, and that the frequency of shaking greatly increased before each mating flight and subsided again afterwards. Following the final mating flight shaking was still observed but gradually became gentler and less frequent, and ceased altogether when the queen started laying.

Taking these two sets of results in conjunction we have a picture of queens being shaken only at the swarming and mating seasons, and not during the rest of the year. Furthermore, the frequency of shaking rose to a peak just before the queens left the hives with the swarms, and also just before they went out on mating flights. It seems, therefore, that there must be a connection between the flights of the queen and shaking, and that the shaking of the queen may, in fact, be a mechanism to cause her to leave the hive at the appropriate time.

STUDIES ON THE ORGANISATION AND EVOLUTION OF COURTSHIP BEHAVIOUR PATTERNS IN *Drosophila*

By M. BASTOCK
London
and A. MANNING
Edinburgh

No précis of this paper was available at the time of going to press.

TWO ASPECTS OF THE BEHAVIOUR OF *Aleochara bilineata (Coeleopt)*

By C. D. PUTNAM
Cambridge

A full account of this work will appear in a later issue.

BOOK REVIEWS

British Medical Bulletin Vol. 12, No. 1 (*Recent Research on Vitamins*). 1955. 15s.; Vol. 12, No. 2 (*Neuro-otology*.) 1956. 15s.; Vol. 13, No. 3 (*Autonomic Nervous System*.) 1957. 20s. London: Medical Department, British Medical Council.

These additions to what is now a recognised and respected journal maintain the high tradition that is to be expected from earlier issues. The publication on vitamins, which forms a memorial number to Sir Edward Mellanby and has enjoyed the scientific editorship of Prof. B. S. Platt, is a veritable text-book in miniature, and provides in readable if compressed form a wealth of information on vitamins in relation to protection of the liver (C.H. Best, *et al.*), the blood and gastrointestinal tract (L. J. Witts), nervous system and skin (H. M. Sinclair), bones (W. I. M. Holman & R. A. McCance), vision (Antoinette Pirie), tissue cultures (Honor Fell), carotenoids (R. A. Morton & T. W. Goodwin), animal nutrition (Marion Coates, *et al.*), antivitamins, antimetabolites and chemotherapy (A. Albert), and other topics. L. W. Mapson describes the effect of processing on the vitamin content of foods and other contributors include Dame Harriette Chick, Sir Rudolph Peters, Sir Charles Harrington, Margaret Hume, T. Moore, C. E. Dalgliesh, E. Lester Smith and L. J. Harris. Perhaps the best tribute that could be paid to this number is to say that the reviewer has not infrequently employed it for reference purposes since its appearance.

The other two issues deal with topics that, in many instances are of much direct interest to behaviourists. Thus the number dealing with neuro-otology contains, *inter alia*, sections on electrophysiology of the central auditory pathway (I. C. Whitfield), the comparative physiology of the otolith organs and the peripheral mechanisms of equilibrium (both by O. Lowenstein), loudness recruitment (M. R. Dix), fatigue and adaptation of hearing (J. D. Hoor) and the investigation of vestibular function (T. Cawthorne, *et al.*).

The autonomic nervous system is discussed in 14 sections, ranging from acetylcholine metabolism at nerve-endings (R. I. Birks & F. C. MacIntosh) and the formation of catechol amines in the animal body (H. Blaschko) to sweating and sympathetic innervation (C. Lovatt Evans).

A.N.W.

The UFAW Handbook on the Care and Management of Laboratory Animals. Edited by A. N. Worden and W. Lane-Petter. London: UFAW. Second Edition, 1957. Pp. xix + 951. 70s.

The second edition of this valuable work appears ten years after the first, and its greatly increased size is a measure of the growth in knowledge of the subject that has taken place in the interval. The editors are to be congratulated on the completion of their task which has involved the collection and collation of seventy-five chapters from nearly ninety contributors; their labours have resulted in a volume indispensible to every experimental labaratory, and in which few enquirers will fail to find the information they seek.

The book is divided into two parts, the first dealing with general considerations, and the second with individual species or groups of species. In Part I the most important chapters are those on the animal house and its equipment, on nutrition, and on breeding methods. That on equipment is particularly full and very well illustrated with diagrams and photographs; the information has been collected from many sources, and the apparatus and procedures recommended represent the best practice based upon very wide and varied experience. Although diets for each species are dealt with in the individual chapters on them, the chapter in Part I that treats of nutrition generally contains much useful information about the composition and standardisation of feeding stuffs, and an interesting section on diet as an environmental component in which it is pointed out that "it has long been recognised that an animal lacking one or more dietary essentials, e.g. iron, may acquire these when its surroundings are dirty but may manifest deficiency symptoms if maintained in hygienic quarters." Two chapters discuss breeding methods very fully, the first dealing with genetic, and the second with economic considerations. Many other subjects, including the principles of hygiene, pests of the animal house, methods of handling laboratory animals, anaesthesia and euthanasia are given place in Part I. Although there is a chapter on stock-recording systems, the authors of several chapters also very rightly emphasise the great importance of keeping regular and full records.

Part II deals with laboratory animals species by species. The sections devoted to the more

usual kinds of laboratory mammals are very full and cover every aspect of the maintenance, feeding, and housing of healthy breeding stocks. Information is also provided about many species that are not commonly used in laboratories, at least in this country, and the possibility of using some of them for special projects will no doubt be considered by interested workers. But one cannot imagine that there will be any great rush to adopt the North American Porcupine in spite of the reassurance that although "more than 30,000 very sharp quills comprise a portion of the pelage of the porcupine, nevertheless practice enables this animal to handled easily with little or no discomfort to bare hands." A whole page on quill removal, from human flesh not the porcupine's skin, does little to increase confidence.

Of the birds the fowl, pigeon and canary are those given the most detailed consideration, but there are useful notes on other passerine species. Chapters on the lower vertebrates—reptiles, amphibia, and fish—occupy one hundred pages and gather together a large amount of practical information not readily accessible elsewhere. The invertebrates have less space, and the only species discussed in detail are the House- and Blow-Flies, the Fruit Fly, and the Earthworm. Short notes are given, however, on a considerable number of other species.

The volume concludes with full author and subject indexes, and each chapter carries its own bibliography. In a volume of this size some misprints are inevitable, but those noticed have not been numerous or serious. The printing and general get-up of the book are excellent, but it is a pity that the binding seems hardly strong enough for a volume of its size and weight.

L.H.M.

Britain's Nature Reserves. By E. M. NICHOLSON. London: County Life. 1957. Pp. 175. 65 plates. 30s.

In his preface the author, who is Director-General of the Nature Conservancy, modestly writes: "Somebody had to write this book in order to explain the objects and scope of what may in a broad sense be called Nature Reserves, and especially of the part played in the general movement by the recently created Nature Conservancy. I have taken on this task because it is my good fortune to have seen most of them and to be in touch with their management and progress".

Of the 87 or so reserves in the United Kingdom, 46 are described separately and many of the remainder receive brief mention in a further chapter. The separate descriptions are almost all compressed into a few hundred words each, but they do not constitute a mere catalogue, and are well illustrated. Indeed the amount of valuable information contained in the descriptions of those reserves with which the reviewer is familiar is impressive, and the salient features are clearly set out. Any adverse criticisms can be of a very minor nature only, and do not detract from the value of the work as a whole. Thus the account of the fall in ground level at Holme Fen (p. 82) might take more recent estimates into account.

The growth of interest in nature reserves, and in the work and thought that lies behind their acquisition or development will be enhanced by this useful and attractive publication, to which is appended an abridged bibliography and a list of the addresses of Reserve Managements

A.N.W.

O niekotorykh voprosakh sravnitielnoi fiziologii vysshei nervnoi deiatelnosti (Some questions on the comparative physiology of higher nervous activity). By L. G. VORONIN. *Vestnik Moskovskogo Universiteta*, 1955, No. **4-5**, pp. 207-217.

(Reviewed by George W. Boguslavsky of the Rensselaer Polytechnic Institute, and submitted by D. E. Davis.)

Comparative studies have shown that the conditioned reflex serves as the principle of individual adjustment to environment for animals of different phylo-genetic levels, from vertebrates to higher invertebrates. With regard to lower invertebrates (e.g. coelenterata) the question is still open in spite of some observed phenomena which resemble conditioned reflexes.

A reaction is regarded as a true conditioned reflex if it can be shown to undergo experimental extinction and spontaneous recovery. The two processes have been observed in bees, silkworm, and crayfish. By contrast, reports of conditioning in infusoria, hydra, and ascidia do not adduce the evidence, thus suggesting that the phenomenon is one of a different order.

Attempts to develop conditioned defence reactions in hydra and starfish met with failure. The reaction of hydra to light as CS was unstable, leading to the conclusion of its being a summation reflex rather than a true CR. In the starfish, the observed instances of learning do

not warrant consideration as CR's because of technical difficulties in recording and lack of adequate knowledge of the organism's biology.

Conditioned reflexes in vertebrates and higher invertebrates are established effectively by the so-called method of *runs*—approach to food and avoidance of noxious stimuli. Acquisition of these is known to be accompanied by the four types of internal inhibition: differential, extinctive, conditioned, and delay. The variables of conditioning, investigated in relation to the phylogenetic level of development, are:

1. Speed of acquisition of the CR.
2. Facility in shifting from a positive to a negative response to the stimulus.
3. Ability to maintain such facility in a prolonged series of changing conditions.
4. Discrimination between a complex stimulus and its components.
5. Development of conditioned inhibition.
6. Development of conditioned disinhibition.

* * *

1. *Speed of acquisition of the CR.* This does not vary significantly for all of the species observed. When the laboratory conditions maximally resemble the animal's natural habitat, the number of trials ranges from 5 to 20.

2. *Facility in shift.* In this test the positive stimulus is made negative through non-reinforcement. The trials required by the various species to master the problem are: fish 30-45, turtles 25-50, birds 41-120, rabbits 47-107, dogs 33-36, baboons 9-58, chimpanzees 4-6. The differences are not regarded as significant, except, perhaps, in the case of the chimpanzees. In these, however, the effect may be an artifact due to the animals' age (3 to 5 years), since in a later study of an adult male the shift required 34 trials.

3. *Ability to maintain shifts.* In this test the phylogenetic differences emerge clearly. For fish and turtles repeated adjustments to changes in the cue-value of the stimulus proved to be an extremely difficult assignment. This difficulty is manifested by disruption of CR's and by increase in the time required for each successive adjustment. In birds and rabbits, however, each successive adjustment required less time (especially in rabbits), but the rate of improvement was not pronounced. The most remarkable effect was observed in dogs, baboons, and chimpanzees. Among dogs, for instance, on the 6th shift 1 or 2 presentations of the stimulus sufficed to establish its new cue-significance. Similar effect was observed in baboons and chimpanzees on the 5th shift.

4. *Discrimination between a complex stimulus and its components.* Though such discrimination has been developed in dogs and primates, attempts to establish it in fish did not meet with success. The approach reaction can be easily developed in fish to a complex of light and sound as CS. The individual components, however, do not lose this cue-value after more than 100 unreinforced individual components and their unreinforced simultaneous presentation (130 trials).

5. *Conditioned inhibition.* The procedure in developing this consists of presenting some neutral stimulus along with the positive CS, but without reinforcement. If the two stimuli are presented simultaneously, conditioned inhibition develops in all species at about the same rate, except for chimpanzees who require on the average only 3 trials. If, however, the two components of this combination are presented consecutively, or if they are separated by a pause of 5 to 10 seconds, a stable conditioned inhibition develops only in the primates. In chickens, rabbits, and dogs it is established sometimes after prolonged training, but is highly unstable. For fish and turtles the problem is insurmountable.

6. *Conditioned disinhibition.* This procedure involves pairing of the neutral stimulus, previously used for conditioned inhibition, with the differentiated (negative) CS, the combination being followed by reinforcement. In turtles who had previously developed conditioned inhibiton the effect is destroyed by this new combination. In pigeons and rabbits both the conditioned inhibition and the conditioned disinhibition may be developed, but with some difficulty. In chimpanzees the two effects are established easily.

* * *

Interpretation of these findings is in terms of the adequacy of the organism's neurophysiological endowment for survival in its natural habitat, with reference to the Pavlovian functional scheme of the central nervous system.

G.W.B.

Bird Hybrids. A Check List with Bibliography. By ANNIE P. GRAY. Commonwealth Animal Bureaux. 50s.

This painstaking and comprehensive companion volume to the authoress's *Mammalian Hybrids*, published in 1954, fulfils an equally important need, and Miss Gray deserves the thanks of workers in several fields for a most useful and well documented work of reference,

helpfully annotated. As she herself emphasises, however, "While great care has been taken to ensure accuracy of the compilation, it must be stressed that many of the records rest on very slender foundations, and the reader is strongly advised to consult the literature and use his own judgement in assessing the authenticity of any particular cross."

Classification and nomenclature have been discussed and checked with experts and may readily be followed.

A.N.W.

Hamster Guide. By G. EDGAR FOLK, Jr. Wisconsin: All-Pets Books Inc. 1958. $1.00.

This is another in the extensive series of publications produced by the proprietors of the well-known magazine that deals with pet animals. Some treat their subject superficially, but on balance the series achieves a high standard which this addition maintains.

Dr. Folk, of the Department of Physiology, Iowa State College of Medicine, has collated the contributions of a number of American and British authors and the result is a readable and accurate account for those who wish to keep Golden hamsters as pets.

A.N.W.

The Life of the Shrew. By P. CROWCROFT. With an introduction by Maurice Burton and line drawings by Erik Thorn. London: Max Reinhardt. 1957. Pp. viii + 166. 15s.

Dr. Peter Crowcroft is not only a trained and accurate observer but is also gifted with a flair for exposition. He writes clearly and entertainingly and in this small work he has aptly summarised most known facts and observations relating to Shrews on the British List.

Following an introductory chapter and another on catching and caring for shrews there follow others relating to general behaviour, fighting, reproduction, the activity rhythm, longevity and numbers.

The sections on behaviour are descriptive and no attempt has been made to interpret observations in any detailed ethological sense. Nevertheless, it is clear that there is a fund of interesting material to be obtained from these species, and not the least of Dr. Crowcroft's many original contributions has been his demonstration that, with care and common sense, shrews are quite readily captured alive and maintained satisfactorily in captivity. He is to be congratulated on a useful work that collates his own and other studies in a workmanlike manner.

A.N.W.

Hormones, Brain Function and Behaviour—Proceedings of a Conference on Neuroendocrinology, held at Arden House, Harriman, New York, 1956. Bt. H. HOAGLAND. Ed. New York: Academic Press (London: Academic Books). 1957. Pp. xi + 257.

There were 32 participants in this symposium, several of whom attended also the symposium on 5-hydroxytryptamine noted elsewhere in our columns. Following each of the twelve papers there was an informal discussion that is reported, verbatim, even to the inclusion of an amusing wisecrack by Dr. R. W. Gerard when in the Chair. It seems unfortunate that this same chairman cut short an interesting discussion on post-coital sedation, although rightly distinguishing between cathectic and physical energy, for interesting species comparisons were being made.

The papers and discussions were divided into four sessions dealing, respectively, with the effects of steroid hormones on the nervous system; sex hormones and behaviour; serotonin (as 5-hydroxytryptamine is still customarily termed in the U.S.A.) epinephrine, and their metabolites in relation to experimental psychiatry; and the thyroid and behaviour. A great deal of ground was therefore covered, and it is perhaps somewhat unfortunate that, from the behaviour standpoint, ethology as at present understood was far less adequately represented than physiology.

In the discussion of determinations of sexual behaviour patterns, several speakers drew attention to species differences and to the need to have information from many other species, presumably mammals since other orders were not referred to. Specific variation was again a topic of major importance.

Dr. J. R. Tata's paper on the metabolism of thyroxine and of 3:5:3-triiodothyronine by brain tissue preparations contained interesting original data, and indeed the whole symposium, as now published, will be read with profit by students of behaviour as well as by clinical and experimental endocrinologists.

A.N.W.

5-Hydroxytryptamine: Proceedings of a Symposium held in London, 1-2 April, 1957. Edited by G. P. Lewis. London: Pergamon Press. 1958. 60s.

The mysteries that surrounded the biological roles of 5-hydroxytryptamine, merit a Churchillian description: while it cannot be claimed that this symposium dispelled them to any degree—as Sir Charles Harington hoped in his opening remarks—the present volume nevertheless codifies relevant knowledge and gives verbatim accounts of discussions on a topic that may well prove of considerable significance to behaviourists.

Nearly 50 leading workers participated in this international symposium, held at the Wellcome Foundation and selected by the Coordinating Committee for Symposia on Drug Action. In nine separate sessions, followed by a tenth of general discussion, the occurrence, metabolism action of, and antagonists to, 5-hydroxytryptamine serotoxin were discussed *in extenso*.

Dr. D. B. Brodie, in his contribution on the storage and release of 5-hydroxytryptamine, discussed the possible significance of the release of the free from the bound form in chemical mediation in the brain. The action of reserpine—which also affects the capacity of brain cells to store 5-hydroxytryptamine—was discussed in some detail and it was considered that the concepts of W. R. Hess were of great help in endeavouring to build up a hypothesis of brain 5-hydroxytryptamine action. According to this hypothesis, 5-hydroxytryptamine is identified as a neurohormone involved in Hess's "trophotropic" system, and noradrenaline as the neurohormone of the opposing "ergotropic" system. Miss Marthe Vogt, however, while in agreement with this fact that reserpine released 5-hydroxytryptamine from its site storage in the brain, strongly challenged some of Dr. Brodie's deductions concerning the physiological role of the substance in mental processes.

This volume is excellently produced, although the Subject Index is brief and the Name Index is confined largely to the contributors and omits reference to others whose work is cited in the text.

A.N.W.

Aggression. By J. P. Scott. Chicago: University of Chicago Press. 1958. Pp. 148, 7 illustrations. $3.75.

This booklet, which is one of a series "designed to acquaint the professional biologist with the fruits of research in areas of specialisation other than his own" succeeds admirably in its objective. It reviews in simple language the psychological and physiological factors in aggressive behaviour as well as genetic, social, and ecological aspects. A person conducting active research in this field will not find new material but will be stimulated to examine the whole field and to apply some ideas to human populations. The factual material presented is definitely conservative; only observations confirmed for several years are included. Indeed in some chapters such as "the physiology of aggression" the information is somewhat out-of-date. An area of difference of opinion is the conclusion that aggressive behaviour is learned. Certainly many aspects are learned but until more work is done on mammals isolated from birth the question will be unanswered. Although this book was not written for the investigator of animal behaviour, he will want a copy to lend to his colleagues.

D.E.D.

Hypotensive Drugs. Editor, M. Harrington. London and New York: Pergamon Press. 1958. Pp. x + 222. 50s.

This volume contains the proceedings of a symposium on hypotensive drugs and the control of vascular tone in hypertension, held at the Wellcome Foundation during 1956. The symposium formed a sequel to the previous ones on histamine and on anticholinesterase, and arose at the suggestion of a committee of the Biological Council. Following interesting opening remarks from Sir Charles Harrington, who emphasised the volume of the late Dr. Harold King's contributions, and that of collaboration between workers of different disciplines within the same institute, it was divided into four sessions dealing, respectively, with chemical and biochemical aspects, with the pharmacology of hypotensive drugs, with the clinical application of these drugs, and with the control of vascular tone in hypertension. It is evident that the combined discussions of pharmacologists and clinicians were of great value.

The Chairman's concluding remarks after the fourth session pay special tribute to the rat as an experimental animal in this field, and suggest that many results obtained from use of the tail plethysmograph technique in this species are directly applicable to human hypertension.

A.N.W.

The Neurohypophysis. By H. HELLER, Editor. London: Butterworth's Scientific Publications. 1957. 50s.

This beautifully produced volume contains the Proceedings of the Eighth Symposium of the Colston Research Society held in the University of Bristol during 1956. This was the first international meeting devoted solely to the neurohypophysis and there was an impressive series of 18 papers, each of which is reproduced in full, together with the relevant discussion. It seems clear that findings up to 1956 are recorded, documented and critically discussed, and as such the whole forms an extremely valuable work of reference.

A.N.W.

Electronic Instrumentation for the Behavioral Sciences. By C. C. BROWN & R. T. SAUCER. Springfield, Ill.: Charles C. Thomas. 1958. Pp. 176. 42s.

This slim volume sets out "a summary of requisite background information and physical theory for the understanding of contemporary behavioral instrumentation, together with an exposition of a wide variety of instruments for detecting and recording behaviour." With so wide a scope covered in 160 pages the pace is inevitably fast. The authors recommend the novice to use a fuller text for they are well aware of the scanty coverage of straight-forward theory.

Most of the book is devoted to a catalogue of useful circuits. Almost every circuit is accompanied by a diagram showing component values and a description of how it works. The range covered is diverse and comprehensive. For example in the chapter "Timing Circuits," "flip-flop" and "bootstrap" circuits are discussed. Elsewhere, more elementary circuits, such as power units, oscillators, and relay networks, are discussed in detail. Special mention is made in all cases of their application and limitations.

A chapter on transitor theory is included. This is an excellent introduction to the theory and use of these new components. The last chapter has some brief but stimulating views on workshop equipment and practice.

From what has been said it would seem that this book amply fulfils its stated purpose. However, it must be borne in mind that the beginner will be quite unable to follow the diagrams, as there is neither key to the symbols nor a section explaining the unit abbreviations. The diagrams are by far the weakest part of the book and detract much from the value of the test. At least eight of the 58 diagrams have some fault in labelling or are in direct contradiction to the relevant passages, which they are supposed to clarify. Some other sections, such as that on A.C. theory, would be greatly improved by the inclusion of diagrams.

In conclusion, it may be stated that this book collects together a lot of information dispersed in more advanced works. The authors have, it seems, attempted to cover too wide a field. If the space and energy devoted to the chapters on elementary theory had been spent on extending the explanations on the more advanced circuits and on correcting the errors in both the text and diagrams, the book would be considerably improved.

P.J.W.

Bird Hybrids. A Check List with Bibliography. By ANNIE P. GRAY. Commonwealth Animal Bureaux. 1958. 50s.

This painstaking and comprehensive companion volume to the authoress's *Mammalian Hybrids*, published in 1954, fulfils an equally important need, and Miss Gray deserves the thanks of workers in several fields for a most useful and well-documented work of reference, helpfully annotated. As she herself emphasises however, "While great care has been taken to ensure the accuracy of the compilation, it must be stressed that many of the records rest on very slender foundations, and the reader is strongly advised to consult the literature and use his own judgment in assessing the authenticity of any particular cross."

Classification and nomenclature have been discussed and checked with experts and may readily be followed.

A.N.W.

Comparative Physiology of Reproduction. Memoirs of the Society for Endocrinology No. 4. By I. CHESTER JONES & P. ECKSTEIN, Editors. Cambridge University Press. 1956. Pp. x + 254. 50s.

This memoir is based upon the proceedings of the symposium held at the Department of Zoology of the University of Liverpool during 1954, and the fact that there was some delay in subsequent publication of the 14 papers and accompanying discussions does not detract from a valuable and broad survey, adequately documented. It is unfortunate for the non-specialist reader, or for those attempting to check know-

ledge in a separate field that the titles of papers are omitted from the references.

Reproductive patterns are surveyed in separate chapters for teleost fish (W. S. Hoar), male frogs (G. J. & P. G. W. J. van Oordt), female amphibia (C. L. Smith), reptilia (R. Kehl & C. Combescott), male birds (A. J. Marshall), female birds (W. R. Breneman), and mammals (S. Zuckerman & P. Eckstein). L. Harrison Matthews discusses the evolution of viviparity in vertebrates and E. Witschi the vertebrate gonadotrophins. The effects of sex hormones are then discussed in relation to fish and lower chordates (J. M. Dodd), amphibia (L. Gallien), birds (R. M. Fraps) and mammals (J. H. Leathem & R. C. Wolf,) while, A. Jost contributes a paper on modalities in the action of gonadal and gonad-stimulating hormones in the foetus. The whole forms a wealth of material that should be in the possession of all who are concerned with vertebrate behaviour.

A.N.W.

Guide to the Literature of the Zoological Sciences. By ROGER C. SMITH. Minnesota. Burgess Publishing Company. 5th Edn. Pp. 203. 1958. 28s.

This is what it purports to be—a comprehensive guide to Zoological Literature. Not only does the book tell the reader how to start looking for references but also how to keep his card index, prepare his scientific paper, read his proofs and see that the resulting paper is properly classified in a Library. In addition an outline introduction of systematic works on the major groups is given, but naturally this is biased towards American fauna.

The author states in considering the lists of indexes to periodicals that these are "familiar to most undergraduate students"; if this is true of the American student he must be much more familiar with them than most British undergraduates. However, the fact that this book is a primer for a College course would explain this; few British Universities would teach their students such things in a formal way. As keeping up with the literature is becoming more and more difficult the advice and direction given in this book would be very useful if it were not marred by odd omissions. In giving a short list of major periodicals it is somewhat surprising to find the *Journal of Experimental Biology*, the *Zeitschrift für vergleichende Physiologie* and the *Zeitschrift für Tierpsychologie* left out, as are the *Journal of the Marine Biological Association* and *Animal Behaviour* (under all of its aliases).

This is really a book for Americans but any British zoologists can gain a lot of information from it and wonder at the complexities it reveals.

J.D.C.

A Handbook of Animal Physiology. By E. M. PANTELOURIS. London: Baillière, Tindall & Cox, Ltd. 1957. Pp. viii + 255. 25s.

This work is intended as a general introduction to animal physiology for those who are later to study one or more aspects of this subject for biological, veterinary or agricultural degrees. It therefore covers a wide range of topics in a concise manner, with an admitted bias towards those that tend to crop up on examinations papers. There is a useful reading list, and presumably the book is intended to supplement lectures and practical classes.

It may seriously be questioned, however, whether the uninitiated student will derive as much benefit from this book as the author hopes. Undoubtedly there is a great deal of information that can be reproduced in examination answers, but unless the student is prepared to follow up the references and to read widely he will not find it easy to grasp the real meaning of much that is dealt with. The chapters on energy-yielding processes exemplify this, for they contain a high proportion of paper chemistry with details that one can imagine being learned by heart.

In any revision, some of the figures relating to invertebrates would benefit from being redrawn.

A.N.W.

The Physiology of Fishes. By MARGARET E. BROWN. New York: Academic Press. 1957. Vol. 1. Pp. xiii + 477 and Vol. II. Pp. xix + 526. $12.00

As the editor states in her preface, *The Physiology of Fishes* was originally intended to consist of a single volume, but the mass of material led to a division into two parts, each of 10 chapters. The sub-titles are used in a very broad sense, for the majority of chapters are concerned with both metabolism and behaviour. Primarily intended for those interested in fish and fishery research, the book is written also for general zoologists and comparative physiologists.

There can be no question of the authoritative nature and wide scope of the reviews, which relate to aquatic respiration (F. E. J. Fry), air-breathing (G. S. Carter), cardiovascular system

(J. C. Mott), alimentary system and digestion (E. J. W. Barrington), excretion and osmoregulation (Virginia S. Black), skin and scales (J. van Oosten), endocrine organs (W. S. Hoar), gonads and reproduction (W. S. Hoar), early development and hatching (Sydney Smith), experimental studies on growth (the Editor), biochemical comparison (R. M. Love), nervous system (E. G. Healey), eye (J. R. Brett), acoustico-lateralis system (O. Lowenstein), olfactory and gustatory senses (A. D. Hasler), conditional responses (H. O. Bull), ethological analysis of behaviour (G. P. Baerends), reproductive and parental behaviour (L. R. Aronson), swimbladder (F. R. Harden Jones), electric organs (R. D. Keynes), luminous organs (E. Newton Harvey), pigments (D. C. Fox), colour changes (J. M. Odiorne), water quality requirements and effects of toxic substances (P. Dondoroff), and physiological genetics (Myron Gordon). The compilation and editing of such an array of material call for congratulation, and in so far as each review attempts to codify existing knowledge, and to stress gaps without attempting to speculate on future findings, the whole provides an invaluable reference source.

A.N.W.

Diseases of Pigs. By H. I. FIELD. Bulletin No. 171, Ministry of Agriculture, Fisheries & Food. London: H.M.S.O. 1957. Pp. v + 46. 3s. 6d.

The author is extremely well-qualified to provide this account of pig diseases, and has done so with clarity and with proper emphasis upon environmental factors. Each of the common pig diseases encountered in the U.K. is dealt with in turn, in a manner that must be intelligible to the intelligent farmer, and the limitations of present knowledge are emphasised.

The growing prevalence of agalactia and other conditions that cause trouble or losses "around farrowing time" suggests that pigs in their own right, as well as poultry, merit the attention of behavioural studies.

A.N.W.

Behaviour Mechanisms in Monkeys. By H. KLÜVER. Chicago: The University of Chicago Press. 1957. Pp. xxiii + 387. 49s. net.

This is the second impression of the well-known work, first published in 1933 and described by Lashley as having set a new standard for analytic studies of behaviour. In a new preface, the author refers to the fact that behavioural aspects in monkeys have become of interest in laboratories as different as those at the School of Aviation Medicine, Randolph Field, Texas, and at the Virus Research Institute, Entebbe, Uganda, and to the references to simian or primate behaviour even in such morphological works as those of W. C. Osman Hill. The remainder of the introduction is devoted mainly to a brief mention of the author's original contributions since the monograph first appeared. These relate mainly to technique such as those he has described in a series of papers in the *Journal of Psychology* and elsewhere. Special tribute is paid to the late Stephen Polyak.

A.N.W.

Annual Review of Psychology. By P. R. FARNSWORTH & Q. MCNEWMAR. California: Annual Reviews. Vol. 8. 1957. Pp. ix + 502. $7.50. Vol. 9. 1958. Pp. ix + 543. $7.50.

In the latest additions to this well-known series, the chapters on comparative psychology are written by Dr. D. Bindra and by D. W. S. Verplanck respectively. Bindra pays welcome tribute to *Animal Behaviour*, and gives specific notice to the contributions of Dennis, Duckworth & Shirlaw, Kennedy, Steven, Vowles and Wood-Gush. Verplanck's chapter includes a discussion of similar contributions by Hebb, Thornton, J. M. Smith, Stokes, Kerruish, Free, Marter, Wood-Gush & Osborne, Andrew & Wiedemann, and is also of direct interest to British readers since it was prepared following a series of visits to laboratories and field stations, including those of W. H. Thorpe, R. A. Hinde and N. Tinbergen.

Both chapters are critical and useful and should be read by all behaviourists.

A.N.W.

The Life of Mammals. By J. Z. YOUNG. Oxford University Press. 1957. Pp. xv + 820. 84s.

Those familiar with *The Life of Vertebrates* may find the contents of this new work surprisingly different in scope, although the author in his preface states that, in a sense, *The Life of Mammals* forms part of the earlier publication. "The book is meant to be used as a systematic aid to the student of mammals and man who has already some general familiarity with biology. It should serve as a companion to a course of practical study of dissection and of histology and embryology. Drawings of dissection and

sections are included with the hope that they will be found useful in the laboratory."

The approach does not seem to have any parallel among modern texts, and although general as distinct from specialist needs are catered for the work is readable and interesting. Many readers will find it, as doubtless did the author, a useful revision, and students should find facts from scattered sources, gathered together in succinct manner.

The emphasis upon laboratory studies leaves little room for ecological and behavioural considerations, although neural and endocrine mechanisms receive detailed mention.

A.N.W.

The Measurement of Colour. By W. D. WRIGHT. London: Hilger & Watts. 1958. 2nd ed. 52s.

Fourteen years have elapsed since the first edition of this book, and the author has brought matters up to date in a manner expected from long and active participation in this field. It had been hoped that the Commission Internationale de l'Eclairage would reach a decision about a possible revision of the standard observer data in time for its inclusion in this new edition, but this did not prove to be the case, and the author has therefore described in somewhat greater detail than in the first edition the experimental observations upon which the 1931 observer was founded.

Other changes include a separate chapter on three-colour reproduction, containing a section on colour television, and an account of the investigations of Dr. W. L. Stiles and his colleagues at the National Physical Laboratory on a new determination of the colour-matching function. The book is so written as to be intelligible to the non-physicists, and indeed has a clarity that indicates authority. All who employ or are concerned with colour measurement in behaviour or psychology will find it a standard text.

A.N.W.

The Wandering Albatross. By W. JAMESON. London: Hart-Davis. 16s.

Admiral Jameson has been a fascinated student of the largest of seabirds and most skilled of avian aeronauts since he first saw albatrosses from H.M.S. *Ark Royal* in the South Atlantic Ocean.

Majestic and voracious at sea, calm and tame on its breeding grounds, where it performs a spectacular and prolonged nuptial display before mating, the albatross is indeed a worthy subject for study. It lives and can only live in the windiest parts of the world, using the wind to keep it gliding for hours without ever flapping its wings. Perhaps the best chapter in the book is that describing the technique by which it can maintain its height and position by using the varying speeds of different layers of air, and discussing the aerodynamics of this soaring flight. There is also an erudite and most entertaining chapter of research into the history of the fables about the bird. The author finds that, whereas many another bird had some superstition attached to it, no one had any compunction about killing albatrosses until Coleridge wrote *The Ancient Mariner*—sometimes it was even lucky to do so. The author has no personal acquaintance with the albatross on its breeding grounds in the remote islands of the sub-Antarctic, but he ably summarises the writings of other authors who have been more fortunate. The book is illustrated by numerous excellent photographs, and beautiful line drawings by Peter Shepheard.

L.H.M.

Curious Naturalists. By N. TINBERGEN. London: Country Life. 1958. Pp. 280. 25s.

This work is a happy combination of the scientific and the popular, being full of information for the student of animal behaviour and fascinating to the interested layman. The author is so obviously fond of the animals he studies, and refrains from anthropomorphological treatment, even though he explains animal behaviour in human terms. A considerable part of the book deals with insect studies, conducted in Holland, while the remainder is largely concerned with observations on birds, many of them in England.

The hunting wasp, *Philanthis triangulum*, has a multiple track mind, but only one track will function at once, so that at one point the insect is acting on information derived from the scenting organs, and when this has brought it nearer its prey, it turns over to sight, and finally touch. While it is acting on one set of impulses, information from the other sensory organs is ignored.

The brain of the bird would appear to run a system similar to that of the insect C.N.S., but of course on a higher level. This is well illustrated by reference to conflict situations and to displacement activities.

The structure of the book is not as good as its content. It appears to start off as an autobiography, with the author's early studies on hunting wasps, followed by an interlude relating to observations on Snow Buntings in Greenland. Then the work of others is introduced, and these chapters are not quite so interesting, lacking the beautifully described backgrounds of the author's own work. The author writes excellent English, particularly for one not brought up in an English-speaking country, and the frequent photographs are superb and beautifully reproduced. B.A.N.

BOOKS RECEIVED

The following books have been received and in appropriate cases will be reviewed as space permits.

Dorothy & Laurence Horswell (1958)
Pet Dachshund
Fond du Lac, Wisconsin: All-Pets Books, Inc. $1.00

Dalbir B-indra (1959)
Motivation
New York: The Ronald Press. Co. $5.50

Harry F. Harlow & Clinton N. Woolsey (1958)
Biological and Biochemical Bases of Behavior
Madison, Wisconsin: University of Wisconsin Press $8.00

R. H. Smythe (1959)
Clinical Veterinary Surgery Vol. I.
London: Crosby Lockwood 42s.

Andre Voisin (1959)
Grass Productivity
London: Crosby Lockwood 50s.

Jean Delacour (1959)
Pheasant Breeding and Care
Fond du Lac, Wisconsin: A.l Pets Books, Inc. $4.00

Maurice Burton, D.Sc. (1959)
Phoenix Re-born
London: Hutchinson & Co. 25s.

E. N. T. Vane (1959)
Guide to Lovebirds and Parrotlets
London: Cage Birds 12s. 6d.

Annual Review of Psychology Vol. 10
(editor: P. R. Farnsworth)
Palo Alto, California: Annual Reviews, Inc. $7.50

J. B. Free & C. Butler (1959)
Bumblebees
London: Collins 25s.

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EDITORIAL

Contributions to the Journal

The *Notice to Contributors* on the inside front cover of the present issue contains several amendments, the most important of which relates to a new section to be entitled *Brief Communications*. It has been apparent for some time that there is considerable disparity between the lengths of many papers submitted for publication, and that in some instances the shorter contributions would in other journals qualify for a special section. In deciding to inaugurate *Brief Communications*, the Editors and their advisers have been mindful of the possible disadvantages that might result from wrongful usage of such a section. They therefore wish to emphasize the relevant sentences in the *Notice*, viz. "Interim reports will not normally be accepted for this section, which is intended for short papers dealing with the results of completed work, descriptions of techniques, short descriptive notes on behaviour and brief accounts of studies that—for valid reasons—cannot be completed but are clearly worthy of being placed on published record". In this category might well be included negative results the brief publication of which, while not in itself advancing scientific knowledge significantly, might deter others from the fruitless repetition of the same venture. Members of the Association for the Study of Animal Behaviour and of the Section of Animal Behaviour and Sociobiology (Ecological Society of America and the American Society of Zoologists) are reminded that short abstracts of papers presented at meetings of their respective societies are printed in the Proceedings within the Journal.

Consideration has been given to the use of abbreviations, and to nomenclature in general, and the present conclusions are summarised in the single sentence at the end of numbered paragraph 3 in the *Notice*, viz. "All abbreviations and specialised terms or symbols (other than simple metric abbreviations) must be defined." Terms or expressions requiring abbreviations should, at their first use, be given in full, followed in brackets by the intended abbreviation, which may subsequently be used alone throughout the rest of the paper. It is felt that to go further at this stage, and to permit for example even relatively simple psychological abbreviations without definition, would not be without drawbacks. The linguistic circumstances that Bismarck regarded as of such great significance have facilitated the recent translation of this Journal into its Anglo-American form: within them, however, wide technological gulfs remain unbridged.

We are still seeking for a common language as between neuro-physiologists and ethologists. An even greater need is for mutual understanding between psychologists and zoologists—as Hebb has elsewhere emphasised. Until those from different disciplines can present the results of their behavioural studies in such a way that others can interpret them readily we shall do well to avoid terms that may be misunderstood.

UNITARY DRIVES

By R. A. HINDE

Field Station for the Study of Animal Behaviour, Madingley, Department of Zoology, Cambridge

I. General

It is necessary, in any science, to re-evaluate at frequent intervals the concepts used to describe and explain natural phenomena. The concepts of mass, the atom, and the species, to cite a few at random, have been essential tools at certain stages of analysis, but must be qualified, revised or superseded as analysis proceeds. In the study of behaviour, terms such as "drive," "motivation" and "mood" occupy such a position: while they have been invaluable in some contexts, they may hinder progress if used inappropriately. Two difficulties with drive concepts were discussed in previous papers. First, the term drive as used by ethologists has frequently been associated with hydraulic or electrical models of motivation: this has led to confusion between the properties of the model and those of the original (Hinde, 1956). Second, for any pattern of behaviour a number of characteristics may be chosen for measurement, but the correlation between them is often small. The properties of the nervous mechanisms on which they depend thus presumably vary independently, so that the statement that an animal has a strong or weak drive is an inadequate description: use of a simple drive concept thus inevitably leads to an over-simplification of the mechanisms underlying the response (Hinde, 1954a and b, 1958a).

This paper is concerned with related topics—namely various ways in which simple drive concepts can hinder analysis by suggesting an over-simplification of the causal mechanisms underlying behaviour. Drive concepts often acquire, like the "atom" and the "species," a unitary quality—they appear as unanalysable elements in a causal network. Thus "the drive" is spoken of as being increased or decreased, or as activating a group of behaviour patterns. Whether they are used as intervening variables in a mathematico-deductive system, or as constructs to which some degree of physiological reality is imputed, they are regarded as units.

In spite of this, drives are invoked to explain diverse characteristics of behaviour. For instance:

1. Changes in responsiveness to external stimuli. With otherwise constant external conditions, a given stimulus may evoke responses differing either in intensity or kind at different times.

2. Apparent spontaneity. Behaviour may be apparently spontaneous—it may change without apparent alteration in the external stimulus situation.

3. Temporal persistence of the effects of stimuli and of activities. Stimuli may be ineffective when first presented, and only later influence behaviour. It thus appears that their effects are stored. Further, once evoked, a given pattern of behaviour may persist for some time after the stimulus is removed.

4. Temporal grouping of activities. The various patterns of behaviour in an animal's repertoire do not appear at random, but in functional groups. This could be due to each pattern bringing the animal into the stimulus situation for the next (chain responses), or to the various patterns sharing causal factors, or both. In the latter cases they may be spoken of as having a common "drive".

5. Directiveness. The statement that behaviour is directive may imply either that it continues until a certain goal stimulus situation is achieved, or that variable means (i.e. more than one type of behaviour, characterised objectively) are used to a constant end. Some authors describe such behaviour as being associated with "motives" and not merely with drives (e.g. Peters, 1958).

6. Occurrence or manifestation of learning. Modifications in behaviour resulting from experience depend on the internal state of the animal. Many theorists believe that "drive reduction" is essential for learning to occur. This question is mentioned only incidentally in this paper.

A unitary concept of drive implies that these diverse characteristics of behaviour depend on the same features of the underlying mechanism, but there is no a priori reason why this should be so. Indeed, even when it is used solely to account for changes in responsiveness to a constant stimulus, a unitary drive concept may conceal the diversity of the causes of changes in behaviour. Evidence for this view is presented in this paper. It is drawn from several vertebrate

groups, and thus involves phyletic leaps from one type of nervous system to another, but at this stage it seems fruitful to draw evidence from a reasonably broad comparative basis. In other respects the discussion here is selective—a few topics of interest to ethologists have been chosen: reviews and discussions of drives and drive concepts are available elsewhere (e.g. various papers in Nembraska symposia on motivation, 1953 *et seq.*; Hilgard, 1948; Peters, 1958).

II. The Diversity of Drive Concepts

Naturally the concepts used by different authors differ widely—"drives" may refer to stimuli, responses, physiological states, psychological states, mathematical intervening variables, or to compounds of these. It would be irrelevant to attempt to classify these here, but it will be necessary to distinguish clearly between concepts which refer to extraneural states or stimuli (e.g. Miller & Dollard, 1941) and those which refer to intraneural states which may or may not depend on extraneural factors (e.g. many ethologists). Clearly these have different properties.

Two further distinctions must be mentioned. The first concerns "biogenic" and "psychogenic" drives. In the former, fluctuations in behaviour are related directly to changes in the internal state of the animal. Thus the "feeding drive" depends on preceding deprivation, and the "sex drive" on androgens in the blood stream.* However, not all behaviour has been related to extraneural states or stimuli, and it is improbable that it will be. In such cases motivation has been inferred whenever behaviour changes. This may be valuable at a descriptive level, but can lead to the postulation of an almost limitless series of "psychogenic" drives—social, exploratory, manipulatory, and so on (see Thorpe, 1956). Such postulated drives help in understanding the causal basis of behaviour only when further predictions, made on the basis of the known properties of "drives", can be tested. This distinction between biogenic and psychogenic drives has been useful in that behaviour dependent on biogenic drives is more easily manipulatable by the experimenter, and has been more actively studied. It breaks down, however, in that most behaviour depends on both biogenic and psychogenic factors (Hebb, 1949).

*In such cases some authors use "drive" to refer to the extraneural factors themselves (e.g. Nissen, 1958) or to a state closely related to them (Hull, 1943), others use it to refer to a state of part of the nervous system induced by these extraneural factors (e.g. Tinbergen, 1951), and others to refer to both (Thorpe, 1951). In the latter cases varying degrees of neurological specificity may be imputed to the drive.

A third distinction concerns the precise roles played by drives in governing behaviour. Drive concepts are used both with reference to the energising of behaviour and to its control—that is, the determination that this pattern of behaviour shall be shown in given circumstances and not that. In most theoretical systems these two aspects are interwoven—thus the Hullian drive both energises and, via the drive stimuli which result from it, directs, the behaviour. On the other hand, the several "instincts" of McDougall and the "motivational impulses" of Tinbergen are essentially driving forces.

III. Drive as a Blanket Variable

We have seen that the drive concept is used with reference to several properties of behaviour. These, however, may depend on different features of the underlying mechanism: there is thus no a priori reason why the drive should be "unitary."

Consider first the "after response"—the temporal persistence of an activity after the stimulus is removed. The mobbing response of the Chaffinch (*Fringilla coelebs*), for instance, may persist for a minute or two after the predator which evoked it has disappeared. This sort of phenomenon is sometimes explained as being due to a "persistence of the drive." There is, however, no reason for thinking that what persists is the same as the internal state necessary for the initiation of the response: the two may occur at quite different stages in the underlying mechanism. The case may be compared with an engine driving a machine via a flywheel: if the engine is switched off, the rotation persists because of a property of part of the mechanism (flywheel) quite different from that which initiated the rotation (cylinders, etc.).

In practice the after response may be but a special case of the fluctuations which occur in the frequency or intensity of any activity when the eliciting factors are constant. For instance, the singing of chaffinches is known to be influenced by certain internal factors (male sex hormone) and certain external factors (a perch in its own territory, the song of a rival male, etc.). In a sound proof room these are, presumably, constant, but the singing consists of a complex pattern of bursts of song, and bursts superimposed on bursts. There are, of course, changes in the stimuli impinging on the bird (e.g. skin

stimuli, proprioceptive input, etc.), but these are not known to affect singing specifically, and can be assigned at most an inhibitory or permissive role. The patterning of songs must be ascribed in part to inhibitory and facilitative effects which accompany the utterance of each song (Hinde, 1958b)—thus the fluctuations in strength (one property of behaviour drives are supposed to explain) depend on different factors from those controlling its initiation (another property of behaviour ascribed to the drive).*

As a second example of the use of a unitary drive concept to explain diverse properties of behaviour, which may well depend on different aspects of the underlying mechanism, we may consider the directiveness of behaviour. Most complex behaviour is directive in that the behaviour continues and may be varied until a constant end or "goal" is achieved. Goals may be defined in three ways:

1. The goal stimuli produce a decrease in the activity.
2. The behaviour is controlled by the difference between the stimuli impinging on the animal and the goal stimuli.
3. Learning is associated with, or becomes manifest with, the perception of the goal stimuli.

None of these criteria imply that goals play a part in initiating behaviour. However, since (*a*) drives are postulated in connection with the initiation of behaviour, and (*b*) most drive-initiated behaviour is directive, drives are sometimes held to be directive. This may be true in the sense that once such behaviour is initiated, the goal is determined; but it would at the same time seem fruitful to maintain a distinction between the factors responsible for the initiation of behaviour and the mechanisms controlling its directiveness. If the drive is regarded as an extraneural state—as is possible on the Hullian scheme—no confusion arises here. If, however, "drive" refers to an intraneural state, some authors assign to it both the initiation and the directiveness of behaviour. Thus Thorpe (1956), who equates internal drive with patterns of activity in the c.n.s., believes that there must be "within the drive itself some inherent directiveness . . . perhaps identical with (the) expectancy and insight". Thorpe's arguments for emphasising the goal-seeking nature of instinctive behaviour are weighty, but it seems unnecessary to stretch a unitary drive concept to cover this directiveness. We may consider briefly three conceptual schemes which deal with the directiveness of behaviour, but maintain a distinction between the initiating and directing factors.

1. The von Holst & Mittelstaedt (1950) Reafferenz model is concerned with the manner in which behaviour is controlled by the difference between the stimuli impinging on the animal and the goal stimuli. They suggest that an "efference copy" in the motor centre is potentially nullified by "reafference" returning from the effectors and exteroceptors as a result of the movement. Only when the two exactly compensate for each other does the movement cease.

2. Hebb (1949) has produced a neurological model in which the initiation and directiveness of behaviour are separated. Emphasising that the central nervous system is continually active, he regards motivation as an organised state of this activity which is responsible for the persistence and directiveness of behaviour and whose stability permits learning to occur. The variability of this activity may be limited by need states, external stimuli, or intraneural factors (e.g. conceptual activities—the model can thus handle psychogenic drives). Later (1955) he discussed the role of non-specific sensory input in maintaining arousal, but this and the details of his neurologising (Milner, 1957) are not relevant here: the point is that he separates the mechanisms controlling the persistence and directiveness of behaviour from the factors which initiate it and the neurological loci at which they act. The need states enter in only as one factor limiting the variability of the organised activity.

3. Turning to a non-physiological model concerned primarily with the occurrence of learning, Meehl & MacCorquodale (1954) have shown how an expectancy theory can be formalised. Suppose we are dealing with the choice point stimulation in a maze (S_1) which, when followed by a right turn (R_1), leads to the food box (S_2). Then in their scheme, reaction potential depends on (*a*) the expectancy, which is a function of the number of times $S_1 \rightarrow R_1$ has or has not been followed by S_2; (*b*) the cathexis of S_2, which in their theory is a function of the number of contiguities between S_2 and the consummatory response, but could be defined in other ways; and (*c*) the need (D), which can be defined by the interval since satiation. Thus the

*We may note here that in some behaviour systems such inhibitory effects are accommodated by additional variables (e.g. reactive inhibition) which affect reaction potential. As discussed later, such inhibitory effects consequent upon performance are complex, and it is doubtful if they can be described adequately in terms of one or two additional variables.

response depends on both "drive" and "expectancy", but expectancy is not "part of" or "within" the drive.

These schemes are cited merely to emphasise that the initiation and directiveness of behaviour can be handled independently. It is not fruitful to stretch a unitary concept of drive to cover both.

We have seen, then, that the several properties of behaviour which the drive concept is used to explain need not depend on the same characteristics of the underlying mechanisms—a unitary concept may lead to over-simplification.

IV. Drive as a Unitary Concept

Introduction

We may now consider the use of a drive concept in a more limited context—namely when it is used with reference to the fluctuations in strength or frequency of a particular activity or group of activities. If the effects of learning, fatigue, etc., are held constant, changes in response strength may be ascribed to changes in drive. Here again, however, various types of evidence suggest that such a unitary drive concept is useful only in certain limited contexts.

Complex Behaviour Sequences

We have seen that one feature of behaviour which drives are postulated to explain is the temporal correlation between functionally related activities. Most behaviour consists of sequences of different activities, and it is often suggested that these occur together because all are governed by the same drive. Thus the nest-building of canaries can be analysed into gathering material, carrying it to the nest, and sitting (building) in the nest. These activities fluctuate more or less together, and we could say that all are governed by the nest-building drive. Indeed they do share causal factors, for all are influenced by oestrogen (Warren & Hinde, 1959), and inhibited by stimuli from the nest. But the correlation between them is not absolute, each has causal factors specific to it, and to account for the pattern of change-over from one activity to the next it is necessary to postulate that the performance of each is accompanied by a self-suppressing effect (Hinde, 1958a). Are we then to postulate a separate drive for each of these activities? If so, where is the process to stop, for each of these activities can be analysed into constituent movements? The usefulness of any concept of a unitary nest-building drive disappears at this stage in the analysis.

Tinbergen (1951) meets this difficulty by postulating a hierarchical scheme of nervous centres, each (except for the uppermost one) receiving "motivational impulses" from its superordinated centre as well as being influenced by factors specific to it. This model has been of value in stimulating research, but cannot be regarded as an accurate picture of the physiological processes involved (e.g. Hinde, 1954a, 1956). In it the "drive" is equated with the "loading" of a "centre" with "motivational impulses": this will be discussed further below.

Mode of Action of Eliciting Factors

It is customary to group the factors which influence the appearance of an activity as independent variables: upon these the drive variable is supposed to depend. This category, however, is a heterogeneous one, for such factors act in diverse ways. We may consider the cases of external sensory stimuli and hormones. The former may:

1. Elicit a response directly—thus a hawk passing overhead elicits fleeing and freezing from a passerine bird (Marler, 1956).
2. Change the readiness to respond to another or the same stimulus. Thus a passerine territory owner must normally be in its territory if it is to attack another male. Usually these releasing (1) and motivating (2) effects of stimuli are difficult to separate, and the behavioural distinction may not represent a difference in mechanism (Hinde, 1954a). The distinction depends, in fact, on an energy storage model of motivation, the stimuli being thought of as either contributing to the store or releasing it. It is thus similar to the distinction, discussed below, between energising and controlling factors—a distinction which may also prove superfluous.
3. Exert long term motivating effects, acting via a pituitary mechanism (Harris, 1955) to affect the internal state (e.g. Marshall, 1954).
4. Influence the orientation rather than, or as well as, the elicitation of the response (examples in Tinbergen, 1951).
5. Exert a non-specific arousal effect (see Section V).
6. Cause a decrease in response strength, either directly, or by eliciting an incompatible pattern. Often the distinction between these two is not easy to make. However, both injections of milk into the stomach, and the inflation of a balloon inside the stomach, reduce eating by hungry rats, but the mechanism by which they

do so probably differs. Milk injections can serve as reinforcement for the learning of an instrumental response, but inflation of a balloon will not, and may affect eating by inducing nausea (Miller, 1957).

The mechanisms by which hormones affect behaviour are similarly diverse (cf. Beach, 1948). They may:

1. Influence the general condition of the animal—its metabolic rate or muscular strength.

2. Influence the growth of morphological structures concerned in the behaviour (e.g. sexual characters).

3. Influence the interoceptive stimuli received from organs concerned in the response. Thus prolaction affects the parental feeding of the ring dove partly by its effect on crop growth (Lehrman, 1955), and androgens influence the copulatory behaviour of rats in part through their influence on the sense organs of the glans penis (Beach & Levison, 1950).

4. Produce specific effects in the c.n.s. directly. Thus implantations of very small amounts of stilboestrol dibutyrate in the posterior hypothalamus, but not elsewhere in the c.n.s., lead to the full development of sexual behaviour, although the genital tract remains anoestrous (Harris et al., 1958).

5. Produce a non-specific effect via the brain stem reticular system (see below, and Dell, 1958).

6. Influence the production of other hormones.

Even when the effect is directly on the c.n.s., its precise nature is not clear. Often it seems that the hormone has the effect of an internal stimulation to activity. In some cases, however, it seems rather to influence the range of stimuli which will evoke the response in question. Thus larger doses of androgen will increase the variety of stimulus objects capable of evoking mating in rats without affecting the latency, frequency of copulation, or rapidity of ejaculation (Beach, 1942, 1947; see also Campbell & Sheffield, 1953; Hall, 1956).

Thus the mechanisms by which independent variables affect behaviour are diverse. If the drive concept refers to extraneural factors, then it must be recognised that these affect behaviour in a number of ways. If it refers to a state of part of the nervous system, then a unitary drive concept implies that these various effects are combined in a mechanism central to the final common path, and that response strength depends on the state of this locus. This is discussed in the next section.

The Centre Concept

As we have seen, some authors use a drive concept to refer to the state of part of the c.n.s., usually described as a "centre". In general, four types of property may be ascribed to centres:

(*a*) The various factors influencing the response are combined there. Further, causal factors which act intermittently (e.g. hunger pangs) can produce a continuous effect via the centre, where its effects are stored.

(*b*) It energises the response mechanism.

(*c*) The response strength depends on its state.

(*d*) It welds together individual responses to form a complex reaction pattern.

Centres having some or all of these properties have been postulated, for instance, by Morgan (1943) and Tinbergen (1951). Stellar (1954) goes further and localises the centres in the hypothalamus—"the amount of motivated behaviour is a direct function of the amount of activity in certain excitatory centres of the hypothalamus." Authors disagree, however, about how many of the above properties they ascribe to their centres.

Behavioural evidence adduced for postulating such centres is of three types:

1. The different factors controlling each activity must be combined somewhere. However, this may occur gradually—Tinbergen (1951) suggests in a hierarchy of centres. Certainly there is no evidence that the effects are summated solely in the hypothalamus, as Stellar (1954) suggests. Further, even changes in the final common path may influence the response.

2. Since one factor (e.g. androgens) may influence a number of activities, there must be a centre through which that factor acts (Tinbergen, 1951). This is a non sequitur, for a given hormone may affect diverse structures, neural and non-neural.

3. The impossibility of accounting even for the biogenic drives solely in terms of extraneural irritants (Morgan, 1943). For instance, the local factors (e.g. stomach contractions) proposed by Cannon (1929) in his theories of hunger and thirst are not necessary for motivated behaviour. This, however, is certainly insufficient by itself to necessitate all the above properties.

Although a centre theory may account conveniently for many facts of behaviour, behavioural evidence for centres is by nature indirect. We may therefore consider the nature of the neurological evidence. This is of the following main types:

1. Ablation experiments showing that a particular part of the c.n.s. is essential for a given type of behaviour. In some cases, e.g. hunger and sleep, the behaviour is controlled by two different hypothalamic regions—one with inhibitory and the other with excitatory properties (rev. in Stellar, 1954). However, even if one area is essential for a given type of behaviour, other regions may also be necessary. Further, care is necessary in the interpretation of such experiments—thus a bilateral lesion in the region of the ventromedial hypothalamic nuclei causes rats to over-eat; but nevertheless causes a reduction in bar-pressing (rewarded by food), in tolerance of quinine, in speed of running to food, and so on. The lesions do not have the same motivational effects as a normal increase in hunger (Miller, 1957).

2. Experiments showing that the behaviour is evoked by electrical stimulation of one region and not of others. These may support property (*d*), for stimulation of a small area may evoke the consummatory behaviour of a sequence, the appetitive behaviour which precedes it (Hess, 1943; Hess & Brügger, 1943), and even a previously learnt instrumental response leading to the appropriate reward (food, drink) (Miller, 1957; Andersson, 1958).

However, such evidence does not imply that the intensity with which both appetitive and consummatory behaviour may be shown depend on the state of one locus—behavioural evidence shows that they may vary independently. Thus Kagan (1955) found that male rats allowed to mount females but not ejaculate showed an improvement in maze performance but a decreased tendency to show sexual responses in the goal box (see also Larsson, 1956).

3. Demonstrations that drugs, hormones, solutions, etc., will influence the behaviour when applied to one region of the brain, but not to others (e.g. Miller, 1957; Harris, et. al., 1958). However, such experiments do not show that the effect of *all* motivational factors are combined in this locus.

4. Olds (1958) has shown that electrical stimulation in an area centred round the hypothalamus and including much of the rhinencephalon and parts of the thalamus, tegmentum and basal ganglia, is rewarding, for the animal will learn to press a bar in order to give itself shocks. The cells in this system are differentiated into subsystems, some being sensitive to food deprivation and others to androgens.

In many cases several types of evidence are available for the same hypothalamic locus. Thus stimulation of a certain region in mammals elicits both drinking and a conditioned response previously rewarded by water; and destructive lesions result in hypodipsia (Andersson et al., 1958, working with goats). Drinking behaviour is also influenced appropriately by the injection of minute quantities of hypotonic or hypertonic saline into this area (Anderssòn, 1953; Miller, 1957, working with rats).

The evidence has been over-interpreted, however, in two respects. First, as Stellar admits, the cortex and thalamus may be important in motivation apart from any influence they have on the hypothalamus. Although the rage response of cats is abolished by hypothalamic lesions and evoked by hypothalamic stimulation, and can be shown by cats lacking a telencephalon, the normal response depends on complex interrelations between telencephalon and diencephalon (Bard & Mountcastle, 1948). In particular, the sham rage of hypothalamic animals lacks an after-response—the persistence of the behaviour, one of the characteristics which drives are postulated to explain, is absent. Any one response depends on diverse mechanisms in diverse parts of the c.n.s., and may be influenced by changes in any one of them.

Thus although the close connection between certain areas in the hypothalamus and specific groups of behaviour patterns cannot be doubted, it is also certain that these areas are intimately connected with others which are also essential for the normal response. It must be admitted that most authorities who use a centre concept emphasise that it need not be anatomically localised. However, its utility depends on the homogeneity of the region said to comprise it, for the centre must be in some respects a functional unit, and the concept cannot usefully be stretched to cover functionally heterogeneous and diverse brain regions. It is significant that even behavioural evidence, which at first sight might lead to the postulation of a simple centre, on further analysis demands a more complex nervous mechanism. Thus Beach earlier (1942) postulated a unitary "central excitatory mechanism" for male sexual behaviour, and now (Beach & Jordan, 1956) postulates two—an "arousal mechanism" which mediates the awakening and increase in sexual excitement, and a "copulatory-ejaculatory mechanism" which mediates mounting and intromission. (See also Larsson, 1956).

A second point is that there is as yet no

evidence that hypothalamic centres store energy, electrical charge, or even motivational impulses. Long term changes in behaviour, such as those produced by hormones, may be due to the ease with which neural activity takes one pattern rather than another, and not to any increase in a driving force stored in a centre.

In summary, then, while recognising that there are certain areas which are concerned with specific types of behaviour, it would seem profitable to distinguish between evidence related to coordination (property (*d*)) and that relating to motivation (properties (*a*)-(*c*)). Further, it is clear that changes in response strength may depend on changes in more than one part of the nervous system, and do not necessarily depend on storage of any form of energy in a neurological locus.

Reduction in Responsiveness

We have seen that it is not fruitful to regard response strength as depending on the state of one locus in the c.n.s. The complexity of the factors influencing it can be illustrated by considering changes consequent upon performance. These may be due to:

1. Removal of the eliciting factors.
2. Direct consequences of the movement—fatigue or adaptation effects on muscles, at synapses, etc.
3. New stimuli (interoceptive or exteroceptive), encountered as a result of the movement, which either inhibit the response directly or elicit an incompatible one.
4. Learning, e.g. habituation.

Removal of the eliciting factors includes that of both the precipitating stimuli and the need states, and will not be considered further. Learning is outside the present discussion, but short term learning is inseparable from factors listed under (2). We are thus left with (2) and (3). If drive is considered as an extraneural state, then these are factors which may cause a change in response strength without influencing drive. If drive refers to an intraneural state, then such factors imply that this state is far from simple. We may consider a few examples.

Roberts (personal communication) has recently studied the waning of the withdrawal response of the earthworm. This is a relatively simple response, mediated by the giant fibre system. Nevertheless the response decrement appears to be due to a multiplicity of causes, involving changes in the giant fibre/motor nerve synapse, sensory nerve/giant fibre synapse, in the sensory system, and, at a later stage, in the neuromuscular junction and muscles as well.

In the much more complicated vertebrates we must thus expect a change in response strength to be far from simple. A number of studies confirm this. Eikmann's (1955) work on the prey-catching behaviour of toads indicates a waning which is specific to the point of the retina stimulated, and Franzisket (1953) has shown that the waning of the scratching response of spinal frogs is due in part to changes near the sensory periphery, and in part to more central effects. The importance of effects more or less specific to the stimulus is also shown by Prechtl's (1953) finding that the waning of the gaping response of young chaffinches (*Fringilla coelebs*), which at a certain age can be evoked by visual, auditory and vibratory stimuli, is specific to the sensory modality. The waning to visual stimuli is not due to a retinal effect, for when gaping waned the visual stimuli produced another response—crouching. Similarly, Schleidt (1954) showed that the waning of the gobbling response of turkeys (*Meleagris*) was specific to the tone used to evoke it. "Stimulus satiation" has also been postulated to account for spontaneous alternation behaviour (Glanzer, 1953) and a number of other phenomena. The complexity of the consequences of performance is also illustrated by the mobbing response of chaffinches to predators. To account for all the characteristics of the waning, it is necessary to postulate very short-term (i.e. recovery after a few seconds) short-term (recovery after a few minutes) and long-term (recovery after weeks) effects. Further, in each time range the effects may be positive (leading to an increase in response strength) or negative (leading to a decrease), and may or may not be specific to the stimulus (Hinde, 1954b, in prep.).

Turning to the effects of new stimuli encountered as a consequence of activity, we may consider the control of drinking in mammals.

Miller and his co-workers (e.g. 1957) have shown that there are inhibitory effects on drinking from the mouth-throat region and from the stomach. Their effectiveness varies between species—thus in the dog there are effective mechanisms of inhibition from the alimentary canal (Towbin, 1949), so that after a period of deprivation the animal does not immediately make good its water deficit, whereas the camel (Schmidt-Nielsen *et al.*, 1956) and goat (Andersson *et al.*, 1958) do.

Drinking is also affected by the water balance

in the tissues (Adolph, 1941): this effect probably occurs via a hypothalamic mechanism, for injections of hypertonic saline into the brain ventricles produce both drinking and learned responses previously rewarded by water, and injections of distilled water reduce drinking (Andersson, 1953; Miller, 1957). The mechanisms controlling the cessation of drinking are thus multiple. Further, the rate of decay of the different factors differ, so that their consequences on behaviour are not the same.

Similar data are available for hunger in mammals (Miller, 1957; Smith & Duffy, 1957) and it must also be noted that the control of hunger is further influenced by learning (Hebb, 1949).

Likewise, Precht & Drees (e.g. Precht, 1958), working with Salticid spiders, have shown that responsiveness to models of prey can be reduced either by feeding or by releasing the hunting behaviour frequently without feeding. They distinguish between "drive" which depends on deprivation and "excitatory level" which is a function of non-release of the eating pattern.

In summary, then, we see that a change in response strength may be due to factors of different types operating at numerous stages within the stimulus-response mechanism. Thus, at this stage of analysis it is of doubtful value to ascribe changes in threshold or response strength to changes in the state of one locus in the c.n.s., or solely to a unitary drive.

Furthermore, it is clear that the mechanisms governing the elicitation and cessation of different types of behaviour may have few similarities. For instance, the mechanisms for the control of food and water intake discussed above are clearly different from those which govern the reduction in sex behaviour after copulation (Beach & Jordan, 1956). Generalisations about the nature of drives derived from study of one type of behaviour are thus not necessarily applicable to others.

Dependent Variables

A similar point is illustrated by the small correlation found between different measures of the same "drive." Thus the tendency to show any group of activities can be measured in a number of ways. "Hunger" can be assessed by the amount of food eaten, by speed of running to obtain food, by the intensity of an aversive stimulus which the animal will withstand to obtain food, by an instrumental response, or in other ways. Such methods have been reviewed by Miller (1957) who emphasises that the different techniques do not always agree. Thus in a comparison of three measures of thirst after injections of saline into the stomach, measures of the consummatory response were sensitive only at short intervals after injection, of bar-pressing at longer intervals and of aversion to quinine throughout the range.

Even when one technique is used, a choice of actual measures is open—latency, intensity, frequency, etc. Here again, the correlations between different measures may be low (e.g. Hilgard & Marquis, 1940; Hall & Kobrick, 1952; Hinde, 1954a). These discrepancies between different ways of measuring the same response, and between different measures, are further indications of the complexity of the underlying mechanisms, and throw further doubt on the usefulness of a unitary concept of drive.

V. General and Specific Drives— The "Energising" Function

Introduction

Some theorists use the drive concept only with reference to particular groups of activities—feeding, sex, and so on. The extra-neural irritants are regarded as both energising and channelling the behaviour—e.g. by affecting specific neural mechanisms which mediate particular responses or groups of responses (e.g. Tinbergen, 1951). By contrast, Hull (e.g. 1943) and other workers often regard individual drives as additive, and their "general drive" variable refers to a general state, due to all the specific needs at the time. Discrimination between need states is then due to the drive stimuli associated with the specific hunger, thirst, etc., drives, but the intensity of behaviour depends on the general drive.* Care is thus necessary in the manner in which a drive concept is used—for some authors it refers to factors specific to the behaviour under examination, and for others to non-specific ones. In fact it is now known that stimuli, hormones, etc., have both specific and non-specific effects on behaviour: the part played by the non-specific factors makes it necessary to reconsider the view that drives "energise" behaviour.

*Thorpe (1956) also postulates a "general drive", though of a different type from that of Hull. Emphasizing that perception plays a part in all behaviour, he postulates a general drive, concerned with perception, which "finds its most characteristic expression in exploratory behaviour in all its various forms." It is not necessary to Thorpe's thesis that this general drive actually motivates all behaviour.

Non-Specific Input

The central nervous system can show spontaneous integrated activity without sensory stimulation (Adrian, 1950). This is shown, for instance, by studies on the periodic discharge of the lobster's cardiac ganglion. When the various factors which influence the beat (e.g. chemical milieu, state of heart) are held constant, the ganglion still generates a periodic repeated complex pattern (Maynard, 1955; Hagiwari & Bullock, 1957). For integrated behaviour of the more or less intact animal however, some non-specific sensory input is necessary. Thus the locomotory rhythm of spinal dogfish and the walking of anurans persist only so long as some dorsal roots are intact (Weiss, 1941; Gray & Lissmann, 1940; Lissman, 1946). Similarly, the compensatory movements made by a frog on a tilting table wane less rapidly if the retina is functionally intact even when the animal is in an optically homogeneous field, or in darkness; and they are also influenced by stimuli through dorsal roots 8-10. Extero- and proprio-ceptors work with the eyes in maintaining the "tone" of the neuromotor apparatus for the compensatory movements (Birukow, 1951).

Recently such non-specific effects of stimuli have been studied in mammals in the course of work on the brain stem reticular formation. Sensory input reaches the cortex in two ways—via the sensory projection systems to specific sensory areas, and via a diffuse system of fibres and synapses to wide cortical areas. The latter system serves to maintain a level of activity in the cortex sufficient for messages travelling by the direct system to have their effect (e.g. Adrian, Bremer & Jasper (editors), 1954). It is affected not only by sensory stimuli but also by corticofugal influences (e.g. Hebb, 1955) and by variations in the milieu intérieur (Dell, 1958).

An adequate degree of physiological arousal is thus a sine qua non for organised behaviour. Probably different types of behaviour require varying degrees of non-specific arousal—thus there is a sequential appearance of activities as the body temperature of *Perognathus* rises after hibernation (Bartholomew & Cade, 1957). Indeed there may be an optimum degree of arousal for each activity, performance deteriorating at both high and low levels (Hebb, 1958).*

We see, then, that if the "drive" refers to extraneural factors, we must recognise that they affect behaviour in two ways, specific and non-specific. If, however, we regard the drive as an intraneural state, then again we must regard this as due to, or effective because of, both types of factor. The role of each is considered below.

The "Energising" of Behaviour

Hebb (1955) equates the non-specific factors which are essential for arousal with a general drive. He points out that they do not control which type of behaviour occurs, and suggests that they act as energisers. On such a view the non-specific factors are primarily responsible for the intensity of behaviour, the specific ones primarily for determining which type of behaviour should appear.

An alternative view would be to regard the non-specific factors as necessary merely for the efficient functioning of the control mechanism, the specific ones determining both the nature and intensity of the behaviour shown. On this view the drive, however defined, would act as an energiser for behaviour only in a very limited sense—given continuous central nervous activity the specific factors (stimuli, hormones, etc.) could act merely by increasing the probability of one pattern of activity rather than another (see Hebb, 1949).† Their influence on the intensity of behaviour would then depend on their effectiveness in limiting the activity to one pattern—and for this there may well be an optimum value of the specific factors as well as (as Hebb suggests) of the non-specific ones. We see then that, granted that non-specific input is essential, two views are possible as to its role. On the first, it is the non-specific factors which primarily affect the intensity of particular types of behaviour, even when the animal is aroused, and on the second intensity is primarily (though not necessarily exclusively) controlled by the specific ones.

No experiments with intact, alert and active animals dealing adequately with the effect of factors primarily relevant to one activity on the

*Duffy (e.g. 1957) comes to a similar conclusion—pointing out that a variety of physiological measures show considerable correlation (e.g. heart rate, respiration rate, E.E.G. records, P.G.R. records, etc.), she suggests that they provide an index of "arousal" valid for all behaviour just as loudness can be measured independently of pitch, and that there is an optimum degree of arousal for efficient behaviour.

†Such a view represents a return to the point of view of Lashley (1938), who emphasised that recent physiollogical work made it unnecessary to account for the maintenance of activity, but only for its direction, and that hormones probably act by rendering central mechanisms excitable. Motivation he regards as "not a general drive or libido," but "a partial excitation of a very specific sensorimotor mechanism. . . ."

intensity of another are known to me. Most studies assess the effects of variables on responses already known to be related to them—fear-provoking stimuli on fleeing, or androgens on male sexual behaviour. Little is known, for instance, about the effects of androgens on fleeing. A group of studies showing that, under certain conditions, electric shock or conditioned anxiety may cause an increase in eating or drinking (Webb, 1949; Siegel & Siegel, 1949; Amsel & Maltzman, 1950; Siegel & Brantley, 1951) have been cited in favour of a general drive hypothesis (e.g. by Hinde, 1954) but are open to other interpretations—e.g. an increase could be due to peripheral effects. Further, until the interactions between "drives" are understood in more detail such experiments cannot be interpreted satisfactorily (Verplanck & Hayes, 1953).*

Thus the precise role of the non-specific factors is still not certain. While they are certainly necessary for integrated behaviour, the control of which pattern of behaviour appears is clearly due to the specific factors, and its intensity could be due primarily to the effectiveness of this control. Changes in response strength could be regarded as changes in the probability of one pattern of neural activity rather than another, perhaps revealed by changes in sensitivity to eliciting factors. On such a view we thus need not think of changes in the strength of a response as due to changes in accumulated energy which drives it (cf. p. 135)—and need not think of drives as "energising" behaviour.

This has certain advantages. Thus if the drive refers to external stimuli or an intra-neural state and is thought of as energising behaviour, then the intensity of behaviour must be reduced when drive (stimulation, etc.) is reduced. In practice, as we have seen, there is an optimum level of sensory input for many types of behaviour, performance deteriorating with too much or too little (Hebb, 1955). Further, appetitive behaviour may serve to bring the animal into situations of increased sensory input, as in exploratory behaviour; and very low levels of input may be intolerable to human subjects (Bexton, Heron & Scott, 1954).

Again, on such a view the eliciting factors could be intra- or extra-neural (Lashley, 1938; Hebb, 1949) and the behaviour thus biogenic or psychogenic. In addition, on such a view the moment to moment changes in the intensity or frequency of behaviour such as song could be regarded as due to intraneural changes independent of factors necessary for the initial elicitation of the behaviour, and not to fluctuations in an energising drive (see above, and Hebb, 1949). Finally, such a view could be reconciled with Woodworth's (1918) view that habits acquire dynamic functions, for any response mechanism must have a certain probability of being active. Of course some of the facts just cited could also be reconciled with an energy-storage drive concept—the point made here is that they do not require it.

*Recently Fuster (1958) has shown that both the perceptual and motor processes involved in tachistoscopic perception are facilitated by brain stem stimulation in monkeys.

VI. Conclusion

None of the evidence reviewed in the preceding sections is in opposition to the view that, for many purposes, unitary concepts of drive are an essential analytical tool. Much of all the work in experimental psychology and psychopathology has depended on their use, and their value requires no exposition here.

However, we have seen that the properties of behaviour which drives are postulated to explain are diverse, so that no one drive concept can cover them all. The use of unitary concepts may lead to the construction of over-simple models of the physiological processes underlying behaviour: as the analysis of behaviour proceeds, an analysis of the explanatory concepts is also required. Further, response strength depends on diverse factors and on activity in many different parts of the nervous system, and, indeed, cannot itself be measured in terms of any single parameter. The use of any particular character of the response to assess the strength of a unitary drive involves an arbitrary choice amongst the possible measures. A similar view has also been expressed by Miller (1957), who suggests that a number of controversies (e.g. the role of drive reduction in learning) could be discussed more profitably if the nature of the drive variable was clarified. Finally, since—given the necessary sensory input—the nervous system is continuously active, there may be no need to invoke a drive which energises behaviour. Rather, changes in response strength can be regarded as due to changes in the probabilities of different patterns of activity in the system.

Summary

1. Drive concepts tend to acquire a unitary character—they are regarded as unanalysable entities in a causal network. Nevertheless the

characteristics of behaviour which they are invoked to explain are diverse.

2. The drive concepts used by different authors vary widely. They may refer to extra- or intraneural states. They may be used with reference to behaviour which can easily be related to extraneural factors (biogenic) as well as to behaviour which cannot (psychogenic). Drives may be held to energise and direct behaviour.

3. The several characteristics of behaviour which drives are invoked to explain are likely to depend on different characteristics of the underlying mechanisms. The use of a unitary concept of drive is thus an over-simplification, and may hinder analysis.

4. When learning, etc., is held constant, changes in responsiveness cannot be ascribed to changes in a unitary drive—they depend on complex changes at many different points in the underlying mechanism. Furthermore, response strength cannot be related solely to the state of a unitary nervous centre.

5. External stimuli may have both specific and non-specific effects on behaviour. The latter act primarily to maintain an adequate level of central nervous arousal. The intensity of behaviour depends primarily on the former; and it is suggested that, once the continuous activity of the nervous system is accepted, there is no need to suppose that drives "energise" behaviour.

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REFERENCES

Adolph, E. F. (1941). The internal environment and behaviour: water content. *Amer. J. Psychiat.*, **97**, 1365-1373.

Adrian, E. D. (1950). The control of nerve cell activity. *Symp. Soc. exp. Biol.*, **4**, 85-91.

Adrian, E. D., Bremer, F. & Jasper, H. (1954). *Brain mechanisms and consciousness*. Oxford: Blackwell.

Amsel, A. & Maltzman, I. (1950). The effect upon generalised drive strength of emotionality as inferred from the level of consummatory response. *J. exp. Psychol.*, **40**, 563-569.

Andersson, B. (1953). The effect of injections of hypertonic Na Cl-solutions into different parts of the hypothalamus of goats. *Acta physiol. scand.*, **28**, 188-201.

Andersson, B., Jewell, P. A. & Larsson, S. (1958). An appraisal of the effects of diencephalic stimulation of conscious animals in terms of normal behaviour. *Ciba Symp. Neurological basis of behaviour*. London: Churchill.

Bard, P. & Mountcastle, V. B. (1948). Some forebrain mechanisms involved in expression of rage with special reference to suppression of angry behaviour. *Res. Publ. Ass. nerv. ment. Dis.*, **27**, 363—404.

Bartholomew, G. A. & Cade, T. J. (1957). Temperature regulation, hibernation, and aestivation in the Little Pocket Mouse, *Perognathus longimembris. J. Mammalogy*, **38**, 60-72.

Beach, F. A. (1942). Analysis of the stimuli adequate to elicit mating behaviour in the sexually inexperienced male rat. *J. comp. physiol. Psychol.*, **33**, 163—207.

Beach, F. A. (1947). A review of physiological and psychological studies of sexual behaviour in mammals. *Physiol. Rev.*, **27**, 240-307.

Beach, F. A. (1948). *Hormones and behaviour*. New York: Hoeber.

Beach, F. A. & Jordan, L. (1956). Sexual exhaustion and recovery in the male rat. *Quart. J. exp. Psychol.*, **8**, 121-133.

Beach, F. A. & Levinson, G. (1950). Effects of androgen on the glans penis and mating behaviour of castrated male rats. *J. exp. Zool.*, **114**, 159-171.

Bexton, W. H., Heron, W. & Scott, T. H. (1954). Effects of decreased variation in the sensory environment. *Canad. J. Psychol.*, **8**, 70-76.

Birukow, G. (1951). Studien über statisch-optisch ausgelöste Kompensationsbewegungen und Körperhaltung bei Amphibien. *Z. vergl. Physiol.*, **34**, 448-472.

Campbell, B. A. & Sheffield, F. D. (1953). Relation of random activity to food deprivation. *J. comp. physiol. Psychol.*, **46**, 320-322.

Cannon, W. B. (1929). *Bodily changes in pain, hunger, fear and rage*. New York: Appleton Century Crofts.

Dell, P. C. (1958). Some basic mechanisms of the translation of bodily needs into behaviour. *Ciba Symp. Neurological basis of behaviour*. London: Churchill.

Duffy, E. (1957). The psychological significance of the concept of "Arousal" or "Activation." *Psych. Rev.*, **64**, 265-

Eikmann, K. -H. (1955). Verhaltensphysiologische Untersuchungen über den Beutefang und das Bewegungssehen der Erdkröte. *Z. Tierpsychol.*, **12**, 229-253.

Franzisket, L. (1953). Untersuchungen zur Spezifität und Kumulierung der Erregungsfähigkeit und zur Wirkung einer Ermüdung in der Afferenz bei Wischbewegungen des Rückenmarkfrosches. *Z. vergl. Physiol.*, **34**, 525-538.

Fuster, J. M. (1958). Effects of stimulation of brain stem on tachistoscopic perception. *Science*, **127**, 150.

Glanzer, M. (1953). Stimulus satiation: an explanation of spontaneous alternation and related phenomena. *Psychol. Rev.*, **60**, 257-268.

Gray, J. & Lissmann, H. W. (1940). The effect of deafferentation upon the locomotory activity of amphibian limbs. *J. exp. Biol.*, **17**, 227-236.

Hagiwari, S. & Bullock, T. H. (1957). Intracellular potentials in pacemaker and integrative neurons of the lobster cardiac ganglion. *J. cell. comp. Physiol.*, **50**, 25-47.

Hall, J. (1956). The relationship between external stimulation, food deprivation and activity. *J. comp. physiol. Psychol.*, **49**, 339-41.

Hall, J. F. & Kobrick, J. L. (1952). The relationship among three measures of response strength. *J. comp. physiol. Psychol.*, **45**, 280-2.

Harris, G. W., Michael, R. P. & Scott, P. P. (1958). Neurological site of action of stilboestrol in eliciting sexual behaviour. *Ciba Symp. Neurological Basis of Behaviour*. London: Churchill.

Harris, G. W. (1955). *Neural control of the pituitary gland*. London: Arnold.

Hebb, D. O. (1949). *Organisation of behaviour*. New York: Wiley.

Hebb, D. O. (1955). Drives and the C.N.S. *Psych. Rev.*, **62**, 243-254.

Hess, W. R. (1943). Das Zwischenhirn als Koordinationsorgan. *Helv. physiol. Acta*, **1**, 549-65.

Hess, W. R. & Brügger, M. (1943). Das subkortikale Zentrum der affektiven Abwehrreaktion. *Helv. physiol. Acta*, **1**, 33-52.

Hilgard, E. R. (1948). *Theories of learning*. New York: Appleton-Century-Crofts.

Hilgard, E. R. & Marquis, D. G. (1940). *Conditioning and Learning*. New York: Appleton-Century-Crofts.

Hinde, R. A. (1954a). Changes in responsiveness to a constant stimulus. *Brit. J. anim. Behav.*, **2**, 41-55.

Hinde, R. A. (1954b). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the Chaffinch (*Fringilla coelebs*). I. The nature of the response, and an examination of its course. II. The waning of the response. *Proc. roy. Soc. B.*, **142B**. 306-331, 331-358.

Hinde, R. A. (1956). Ethological models and the concept of drive. *Brit. J. Philos. Sci.*, **6**, 321-331.

Hinde, R. A. (1958a). The nest-building behaviour of domesticated Canaries. *Proc. Zool. Soc. Lond.*, **131**, 1-48.

Hinde, R. A. (1958b). Alternative motor patterns in Chaffinch song. *Anim. Behav.*, **6**, 211-18.

Holst, E. von, & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen zentralnervensystem und peripherie. *Naturwissenschaften*, **37**, 464-76.

Hull, C. L. (1943). *Principles of behaviour*. New York: Appleton-Century.

Kagan, J. (1955). Differential reward value of incomplete and complete sexual behaviour. *J. comp. physiol. Psychol.*, **48**, 59-64.

Larsson, K. (1956). Conditioning and sexual behaviour in the male albino rat. *Acta psychol. Gothoburgensia*, **1**, 1-269.

Lashley, K. S. (1938). Experimental analysis of instinctive behaviour. *Psychol. Rev.*, **45**, 445-471.

Lehrman, D. S. (1955). The physiological basis of parental feeding behaviour in the Ring Dove (*Streptopelia risoria*). *Behaviour*, **7**, 241-286.

Lissmann, H. W. (1946). The neurological basis of the locomotory rhythm of the dogfish. *J. exp. Biol.*, **23**, 143-61, 162-76.

MacCorquodale, K. & Meehl, P. E. (1954). Chapter on Edward C. Tolman in *Modern learning theory*, by Estes, Koch *et al.* New York.

Marler, P. (1956). The behaviour of the Chaffinch. *Behaviour*, Supplement No. 5.

Marshall, A. J. (1954). *Bower Birds*. Oxford.

Maynard, D. M. (1955). Activity in a crustacean ganglion. *Biol. Bull.*, **109**, 420-36.

Miller, N. E. (1956). Effects of drugs on motivation. *Ann. N.Y. Acad. Sci.*, **65**, 318-333.

Miller, N. E. (1957). Experiments on motivation. *Science*, **126**, 1271-8.

Miller, N. E. & Dollard, J. (1941). *Social learning and imitation*. New Haven: Yale Univ. Press.

Milner, P. M. (1957). The cell assembly: Mark II. *Psych. Rev.*, **64**, 242-252.

Morgan, C. T. (1943). *Physiological psychology*. New York: McGraw-Hill.

Nissen, H. W. (1958). Axes of behavioural comparison. In *Evolution and behaviour*, Ed. Roe & Simpson. Yale.

Olds, J. (1958). Selective effects of drives and drugs on reward systems of the brain. *Ciba Symp. Neurological Basis of Behaviour*. London: Churchill.

Peters, R. S. (1958). *The Concept of motivation*. London: Routledge & Kegan Paul.

Precht, H. & Freytag, G. (1958). Uber Ermüdung und Hemmung angeborener Verhaltensweisen bei Springspinnen (*Salticidae*). Zugleich ein Beitrag zum Triebproblem. *Behaviour*, **13**, 143-211.

Prechtl, H. F. R. (1953). Zur Physiologie der angeborenen auslösenden Mechanismen. *Behaviour*, **5**, 32-50.

Roberts, M. B. V. (1959). Ph.D. thesis, Cambridge.

Schleidt, M. (1952). Untersuchungen über die Auslösung des Kollerns beim Truthahn (*Meleagris gallapagos*). *Z. Tierpsychol.*, **11**, 417-435.

Schmidt-Nielsen, B. & K., Houpt, T. R. & Jarnum, S. A. (1956). Water balance of the Camel. *Amer. J. Physiol.*, **185**, 185-194.

Siegel, P. S. & Siegel, H. S. (1949). The effects of emotionality on the water intake of the rat. *J. comp. physiol. Psychol.*, **42**, 12-16.

Smith, M. & Duffy, M. (1957). Evidence for a dual reinforcing effect of sugar. *J. comp. physiol. Psychol.*, **50**, 242-7.

Stellar, E. (1954). The physiology of motivation. *Psych. Rev.*, **61**, 5-22.

Thorpe, W. H. (1951). The definition of some terms used in animal behaviour studies. *Bull. anim. Behav.*, No. **9**, 34-49.

Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen.

Tinbergen, N. (1951). *The study of instinct*. Oxford.

Towbin, E. J. (1949). Gastric distention as a factor in the satiation of thirst in esophagostomized dogs. *Amer. J. Physiol.*, **159**, 533-541.

Ullman, A. D. (1951). The experimental production and analysis of a "compulsive eating syndrome" in rats. *J. comp. physiol. Psychol.*, **44**, 575-581.

Verplanck, W. S. & Hayes, J. R. (1953). Eating and drinking as a function of maintenance schedule. *J. comp. physiol. Psychol.*, **46**, 327-333.

Warren, Roslyn P. & Hinde R. A. (1959). Effect of œstrogen and progesterone on the nest-building of domesticated canaries. *Anim. Behav.*,**7**, 209-213.

Webb, W. B. (1949). The motivational aspect of an irrelevant drive in the behaviour of the white rat. *J. exp. Psychol.*, **39**, 1-14.

Weiss, P. (1941). Autonomous v. reflexogenous activity of the central nervous system. *Proc. Amer. philos. Soc.*, **84**, 53-64.

Woodworth, R. S. (1918). *Dynamic psychology*. New York.

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THE INHERITANCE OF PATTERNS OF SEXUAL BEHAVIOUR IN FEMALE GUINEA PIGS*

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In a previous study, patterns of sexual behaviour were found to differ significantly between inbred female guinea pigs from Strains 2 and 13 (Goy & Young, 1957). In that report a distinction was made between (1) vigour (the frequency or intensity of the œstrous reactions, and (2) responsiveness (the ease with which œstrus is induced by exogenous hormone). Briefly, females from Strain 2 were found to be very responsive to the hormonal treatment, but low in the vigour of their œstrous reactions. In contrast, females from Strain 13 were relatively low in responsiveness but high in vigour. The genetical basis for such a relationship between traits cannot be understood from a study of inbred strains alone. The mode of inheritance of the traits under consideration, and the stability of the relationship under various conditions of hybridization need to be examined. The present experiments were performed as part of a general programme to study the interaction of genetic and hormonal factors in the determination of patterns of sexual behaviour. These experiments have given emphasis to the problem of whether strictly genetic factors or selection factors would account for the inverse relationship between vigour and responsiveness in female sexual behaviour.

As in the study with the male guinea pig (Jakway, 1959), it has been possible to study the inheritance of different elements or components of female sexual behaviour. The observation has been made repeatedly that the female guinea pig displays both a receptive component (the lordosis reflex) and an active component (male-like mounting behaviour) while in œstrus. The mode of inheritance of these two components forms the main body of the present work.

Material and Methods

Previous work indicates that behaviour of spayed females treated with suitable quantities of œstrogen and progesterone is similar to that exhibited prior to ovariectomy (Boling, Young & Dempsey, 1938; Boling & Blandau, 1939; Young & Rundlett, 1939). Largely for convenience, but also to rule out differences in amount of endogenous hormone, only spayed females were used in the present study.

Two hundred and twenty-eight females were used. Twenty-six were from highly inbred Strain 2, 29 from Strain 13, 23 from the F_1 generation, 47 from the F_2, 48 from the backcrosses between F_1 and Strain 2 (B_2), and 55 from the backcrosses between F_1 and Strain 13 (B_{13}). Reciprocal matings were represented in all hybrid populations.

The median age at the time of ovariectomy was 3·5 months in each genetic group. The distributions were not skewed. Eight strain 2 and 8 strain 13 females were spayed at relatively extreme ages (6 to 9 months) and less than 1 month). Previous work has shown that age at the time of ovariectomy does not significantly alter the measures currently being studied (Goy & Young, 1957b). Tests of reproductive performance began one month later on the average. Except where indicated each animal was tested 5 times at intervals of approximately 21 days. For the first 3 tests, each animal was injected with 100 I.U. of œstradiol benzoate followed 36 hours later with 0·2 I.U. of progesterone.‡ For the remaining tests, each animal was injected with 50 I.U. of œstradiol benzoate followed 36 hours later with 0·2 I.U. of progesterone. The volume of all injections was constant (0·5 cc.), and injections were given subcutaneously in the left axilla. Immediately after injection with progesterone, the animals were placed in a standard observation cage (in groups consisting of 6 to 12 individuals) and observed continuously for 14 hours. Each animal was tested once every hour to determine the time of appearance of the lordosis reflex, and its duration was measured with a stop watch on every occurrence. The first

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lordosis obtained was regarded as the onset of œstrus, and animals failing to respond on any of the 14 hourly tests were viewed as not in œstrus. For those animals responding on at least one hourly test, œstrus was regarded as terminated when they failed to lordose on two successive hourly tests.

Control animals from the inbred strains were studied intercurrently with the hybrid generations throughout the course of the study from June 1955, until June 1957.

The measures employed in the present study were the same as those described in detail previously (Goy & Young, 1957a). Briefly, they are as follows: (1) latency of heat; (2) duration of heat; (3) duration of the maximum lordosis; (4) frequency of male-like mounting behaviour; and (5) the percentage of tests on which œstrus was observed (per cent. response). Only the latter measure, in the present study, was employed in those tests following the 50 I.U. of œstradiol benzoate. Eight females from Strain 2 and 10 females from Strain 13 were not tested at this dosage.

The data from the present study were not normally distributed and the variances of the different genetic groups were unequal. Because of these characteristics, conventional parametric analysis was not feasible. Therefore, only X^2 and non-parametric statistics were employed in the analysis.

Results

1. Quantitative Inheritance of the Basic Measures

Strain 13 females displayed a long latency and a relatively short duration of œstrus, a long duration of maximum lordosis, and a large number of male-like mounts during œstrus. Strain 2 females are characterised by a short latency and a long duration of œstrus, a short duration of maximum lordosis, and a general lack of male-like mounting behaviour (Table I). The differences between the inbred strains for these measures is highly significant ($P<\cdot001$) for every measure.

The values obtained for the F_1 resemble Strain 2 for latency and duration of œstrus. For both the duration of the maximum lordosis and the frequency of male-like mounting, the values for the F_1 females are intermediate to the values found for the parent strains. Since no significant differences were found between the reciprocals the results were combined.

In the F_2 generation values highly similar to those obtained for the F_1 generation were found. Again, latency and duration of œstrus resemble those values obtained for the inbred Strain 2. Values for duration of maximum lordosis and frequency of male-like mounting are intermediate to those of the inbred strains.

Within the B_2 population, the values obtained for latency and duration of œstrus and the duration of the maximum lordosis closely approximate those found for inbred Strain 2. On the other hand, mounting behaviour is not reduced to the low level characteristic of the inbred parent strain.

Backcrossing from F_1 to parent Strain 13 (B_{13}) produced females with shorter latencies and longer durations than those characteristic of Strain 13. The values for maximum lordosis and number of mounts were essentially restored to those obtained for the parent strain.

The mode of inheritance of the duration of the maximum lordosis deserves special attention. Table I presents the obtained means from the in-

Table I. Responses of Inbred and Hybrid Spayed Female Guinea Pigs Injected with 100 I.U. Œstradiol Benzoate and 0·2 I.U. Progesterone.

	Number ♀♀	Number tests	% of tests + for œstrus	Latency of œstrus (hours)	Duration of œstrus (hours)	Duration of max. lordosis (seconds)	Number of mounts per œstrus
Strain 2	26	67	94·0	4·2±·19	7·9±·28	13·6±·69	1·0±·27
Strain 13	29	87	79·3	6·6±·26	4·8±·25	24·5±1·34	19·5±3·34
F_1	23	69	98·6	4·8±·16	7·2±·30	19·4±1·29	5·9±1·19
F_2	47	130	95·4	4·7±·13	7·2±·20	19·5±·78	7·1±1·25
B_2	48	144	94·4	4·3±·10	7·9±·22	13·8±·22	5·1±1·31
B_{13}	55	165	86·7	5·7±·13	5·9±·18	22·4±·93	11·5±1·84

breds and crosses. For comparison, means predicted from the assumption of a single gene without dominance are as follows: F_1, 19·1 sec.; F_2, 19·1; B_2, 16·3; and B_{13}, 22·7. The close correspondence of obtained and predicted values strongly supports the assumption of a single gene in the determination of this trait.

Percentage response at 100 I.U. of estradiol, like latency and duration, displays phenotypic dominance of the strain 2 values (Table I). When 50 I.U. of estradiol are injected the same pattern of inheritance is demonstrated: strain 2 (63·6 per cent.), F_1 (62·8 per cent.), F_2 (63·0 per cent.), and B_2 (65·6 per cent); in contrast, strain 13 and B_{13} displayed only 41·9 and 37·9 per cent. response respectively.

2. Independence of the Basic Measures in Mode of Inheritance

Within the parent population as a whole (Strains 2 and 13 combined), duration of œstrus and per cent. response were positively associated and latency and duration inversely related. These associations exist not only between inbred strains, but also within each inbred strain. In addition, the relationship remains essentially unaltered for every genetic group (Table II). Retention of the association in populations of increased heterogeneity suggests pleitropy (multiple manifestations of the same alleles). The common mode of inheritance displayed by these three measures (phenotypic dominance of the strain 2 values) supports the interpretation of a single underlying character. Since latency, per cent. response, and duration of œstrus fail to segregate independently, only the latter measure is used in the remainder of the analysis.

Table II. Product Moment Correlations Between Latency and Duration of Œstrus within each Genetic Group.

Strain 2	Strain 13	F_1	F_2	B_2	B_{13}
—·53	—·79	—·76	—·52	—·64	—·56

Significant negative associations exist between duration of heat and duration of maximum lordosis within the parent population (X^2= 27·69, P<·001). However, genetic independence of these measures is established by the disappearance of any trace of association within the F_1 population and all subsequent crosses. Even within each pure strain the measures are not associated.

3. Analysis of Phenotypic Distributions

The distributions of duration of œstrus, maximum lordosis, and mounting within each genetic group are presented in Table III. The significance of the overall differences among the groups was evaluated by the use of X^2. On this and subsequent X^2 comparisons, expected frequencies of suitable magnitude were obtained by combining adjacent caetgories. For duration of œstrus, X^2 equals 74·02 (10 d.f., P<·001). For duration of maximum lordosis, X^2 equals 77·49 (10 d.f., P<·001). For frequency of mounting, X^2 equals 63·14 (10 d.f., P<·001).

The significance of the differences obtained from relevant between groups comparisons is presented in Table IV. From these comparisons the phenotypic dominance of the strain 2 duration of œstrus is evident. Among the crosses, only the distribution of duration within B_{13} differs significantly from that obtained for the inbred Strain 2. The distribution within B_{13} also differs significantly from that within Strain 13 indicating a retention of the strain 2 value by a significant proportion of the individuals (34·6 per cent.).

For both maximum lordosis and mounting, the distributions within B_2 do not differ from that of the parent strain but do differ from Strain 13. Correspondingly, these distributions within B_{13} do not differ from parent Strain 13 but do differ from Strain 2. Within the other crosses (F_1 and F_2) the distributions differ significantly from both parent strains due to an increase in the proportion of individuals displaying intermediate values.

All of the F_1 individuals have the same genetic constitution. The comparisons between distributions of F_1 and other hybrid groups will therefore serve as an indication of the extent of recombination achieved. Due to the phenotypic dominance of Strain 2 with respect to duration of œstrus, statistically significant reconstitution of the strain 13 type does not appear in the F_2. Instead, the reappearance of the "recessive" parental values for this measure is achieved only among the B_{13} individuals. It should be pointed out that a larger number of individuals would show a statistically significant difference between the F_1 and F_2 hybrids with respect to this trait.

In line with the hypothesis of a single pair of alleles and an intermediate mode of inheritance, the distribution of maximum lordosis ought to display bimodality in the F_2 generation. The failure to achieve this is probably due to the proximity of the modal categories of the parent

Table III. Proportions of Individuals within the Categories Listed for the Various Traits.

	Duration of œstrus in hours									
	2	3	4	5	6	7	8	9	10	11 or more
2	—	—	—	—	—	·423	·269	·115	·154	·038
13	·034	·137	·207	·207	·344	·069	—	—	—	—
F_1	—	—	·087	—	·131	·391	·261	·087	·043	—
F_2	—	—	·021	·064	·255	·212	·255	·149	·021	·021
B_2	—	—	—	·043	·146	·229	·250	·208	·064	·064
B_{13}	—	·018	·127	·237	·272	·218	·072	·036	·018	—

	Duration of maximum lordosis in seconds					
	5 to 9·98	10 to 14·9	15 to 19·9	20 to 24·9	25 to 29·9	30 and above
2	·192	·346	·423	·038	—	—
13	—	·069	·172	·379	·172	·206
F_1	—	·261	·304	·174	·174	·087
F_2	·021	·170	·426	·234	·064	·085
B_2	·104	·604	·250	·043	—	—
B_{13}	—	·127	·272	·237	·200	·163

	Frequency of mounting during œstrus				
	0 to 2·4	2·5 to 4·9	5·0 to 7·4	7·5 to 12·4	above 12·5
2	·804	·154	·038	—	—
13	·034	·137	·172	·137	·158
F_1	·217	·261	·304	·174	·043
F_2	·409	·170	·085	·149	·191
B_2	·583	·146	·083	·041	·147
B_{13}	·218	·127	·182	·164	·309

strains. For mounting activity, where the modal categories of the parent strains are widely separated, bimodality of the trait within the F_2 is achieved.

4. Combinations of Behavioural Components and the Recovery of a New Type

The existence of three independently assorting traits or measures permits the classification of sexual behaviour in a novel manner. Either a high or a low value of any measure may be displayed by a given female. A "high" value is defined as any individual value above the median of the parental population. For the purpose of determining a parental median, the Ns of the two inbred strains were first equalised by random elimination of 3 strain 13 females. With two alternatives for each of three phenotypic elements, 8 distinct combinations are possible. The inbreds and crosses may then be compared on the basis of the frequency with which the different phenotypic combinations are observed.

Table IV. Significance of Differences between Trait Distributions of Inbreds and Crosses.

		2	13	F_1	F_2	B_2	B_{13}
Duration of œstrus	Strain 2		·001	—	—	—	·001
	Strain 13	·001		·001	·001	·001	·05
	F_1	—	·001		—	—	·001
Maximum lordosis	Strain 2		·001	·01	·001	—	·001
	Strain 13	·001		·05	·05	·001	—
	F_1	·01	·05		—	·05	—
Mounting activity	Strain 2		·001	·001	·01	—	·001
	Strain 13	·001		·01	·01	·001	—
	F_1	·001	·01		·02	·001	·07

These sexual behaviour "profiles" for the female are presented in Fig. 1. The behaviour profile most characteristic of Strain 13 falls within the categorical combination labelled "high maximum lordosis (HML), low duration of heat (LD), and high mounts (HMts); for strain 2 females, the modal category comprises the elements of low maximum lordosis (LML), high duration of heat (HD) and low number of mounts (LMts). Each inbred strain occupies relatively few of the 8 possible types. Within the parent population as a whole (P, in Fig. 1) 7 out of 8 possible types are represented. The F_1 crosses neither lose nor add types to the total array, but a significant increase, suggestive of heterosis, occurs in the proportion of females displaying high values on all measures (C.R.= 2·02, P<·05). Within the F_2 crosses, the array of phenotypic combinations is much flatter, and a small number of cases appear with low values on every measure. This proportion, though small, is reliably greater than zero. The identification of females with a phenotypic combination not found in the parent population is expected on the basis of independently assorting genes. The deviation of the obtained proportion below that expected by chance is due to the phenotypic dominance of high values for duration of œstrus.

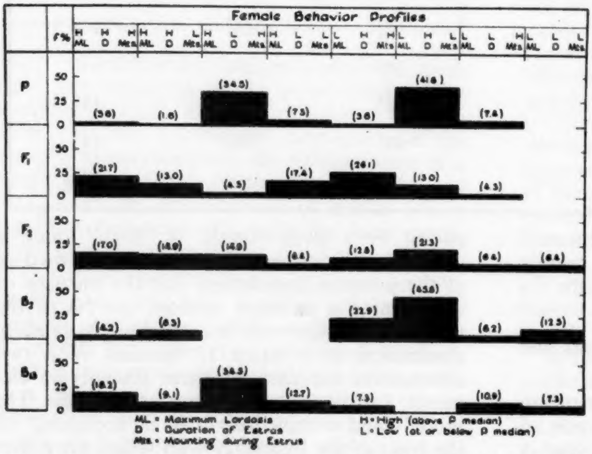

Fig. 1. Frequency distribution of combination of Sexual behaviour traits.

For the B_2 crosses, a significant proportion of females still display the new phenotypic combination. None of the females in B_2 group display the combination most characteristic of strain 13. Correspondingly, the new phenotypic combination is retained in females from B_{13}, but none displays the combination typical of pure strain 2.

Discussion

For the inbred strains, the findings from the present study agree substantially with those reported earlier (Goy & Young, 1957). Latency of heat is considerably lengthened, but both strains show the same increase in latency and the relative difference between the strains remains the same. We are unable to account for the observed increase at the present time but the change is unimportant, regardless of its origin, to the interpretation of the results.

For the present, the precise mode of inheritance of the various components is regarded as significant only in so far as it establishes the independence of the components. There seems little reason to doubt the genetic independence of lordosis and mounting even though each displays intermediate inheritance. For the maximum duration of lordosis only a single or relatively few genetic factors are involved. This is clearly indicated first by the close agreement of means obtained from the hybrids with those predicted on the basis of a single gene without dominance. In addition, the restoration of the values characteristic of the pure strains in the first backcross generation is also indicative of relatively few genes in the determination of the trait. In contrast, mounting does not attain the values characteristic of the parent strains in either backcross group.

The association between a large amount of mounting and a long lordosis, observed within the parent population as a whole, is not maintained in the hybrid populations, again indicating genetic independence of the two components. Thompson (1957) has indicated that, for behavioural traits, covariations may result from four separate sources. These he has called genetic communality, chromosomal cummunality, selection communality, and environmental communality. Chromosomal and environmental communality are excluded as bases for the association since a long lordosis segregates independently of mounting in the hybrid generations.

From such considerations it seems likely that the association resulted from the artificial "selection" of a particular sub-family, or alternatively, only those lines in which the traits were associated continued to reproduce. Supporting the latter possibility is the informal observation that mounting by the female has a facilitating effect on the mating activity of the male. The value of such facilitation for the perpetuation of a strain in which the males are repeatedly characterised as sluggish (Jakway, in press; Valenstein, Riss & Young, 1954; Riss, 1955) is apparent. On the other hand, the ease with which hybrids were obtained from matings between males from Strain 13 and females from Strain 2 indicates that mounting by females is not crucial to mating even though it may be facilitating.

The separateness of the genetic bases for the quantitative aspects of mounting and lordosis is supported by physiological findings. Young, Dempsey, Myers & Hagquist (1938) have shown that the two components are differently related to the ovarian condition at the time of œstrus. The mounting component appears later in ontogeny than the lordosis and mounting is displayed earlier than the lordosis in the cycle of the mature female (Young & Rundlett, 1939). And a few cases have been reported of intact female guinea pigs who mount at cyclic intervals without ever displaying lordosis (Young, 1941).

The present finding provides evidence of separate genetic bases only for the quantitative aspects of mounting and lordosis; whether genetically separate hormonal thresholds exist cannot be determined. The finding has direct implications for our concept of vigour since it shows clearly that the vigour of one component is completely independent of the vigour of the other. This principle, conclusively demonstrated for the female, has been demonstrated in studies on the male also. In a study dealing with the inheritance of the male mating behaviour pattern, different modes of inheritance were demonstrated for ejaculation frequency and rate of intromission on the one hand and the rate of occurrence of the lower components on the other hand (Jakway, in press). Thus vigour of the mating behaviour pattern, as we have come to view it, is not inherited as a unitary trait (i.e. a set of genes regulating the vigour of all aspects of mating behaviour), but rather as a separate set of genetic factors for each of the genetically independent behavioural elements.

In the present study we have been able to record a number of measures which reflect the character of the lordosis reflex. This has permitted us to evaluate both the strength or vigour of that reflex (as measured by the duration in seconds of the maximum lordosis displayed in response to fingering) and also its latency of appearance, the number of successive hours it is displayed, and the per cent. of the tests on which it is displayed. According to the genetic analysis, these four aspects of the lordosis component can be accounted for by two independent genetic factors. The vigour of the lordosis reflex is determined by one of these genetic factors; latency of heat, duration of heat, and per cent. response are jointly determined by the second set of factors as indicated by their common mode of inheritance (phenotypic dominance of Strain 2) and their failure to assort independently during hybridization. Previously (Goy & Young, 1957), "responsiveness" was defined as "a measure of the effectiveness of the hormone in inducing

œstrus, regardless of the character of the induced œstrus." Operationally, the principal criterion was percentage response. In view of the present findings it seems necessary to conclude that latency and duration of heat are also measures of responsiveness to the hormone.

We are unable to account for the findings with regard to mounting behaviour on a strictly genetical basis. When the data for the male (Jakway, 1959) are compared to those for the female, the inheritance of mounting appears quite complex. For in the males, those from Strain 2 exhibit more mounting (Valenstein, Riss & Young, 1954) and a higher rate of mounting (Jakway, 1959) than males from Strain 13. Exactly the opposite quantitative relationships are found for females from these same strains. Possibly alpha-œstradiol benzoate and progesterone produce mounting by acting upon tissues completely different from those acted upon by male gonadal hormone. But the kind of hormone does not appear to be the only factor involved in the low expressivity of this trait in females from Strain 2 (Goy & Young, 1958). For the present, the possibility of modifiers associated with the sex of the individual must be entertained.

Particular attention is called to the finding that the genetic factors controlling responsiveness, maximum duration of lordosis, and frequency of mounting recombine in the F2 population in such a way as to produce a phenotypic combination which is completely new (i.e. without prototype in the parent population). This principle, although well known for morphological traits has never been completely documented for behaviour. Recently, Lorenz (1958) has pointed out the significance of such a principle to the evolution of behaviour and some evidence for the novel recombination of behavioural elements has been obtained by him in studying interspecific crosses. Our findings extend the concept advanced by Lorenz in so far as recombination occurs not only with respect to the presence and arrangement of elements within a pattern of behaviour, but also with respect to the quantitative expression or vigour of the various elements.

Summary and Conclusions

Two hundred and twenty-eight spayed female guinea pigs were used. Twenty-six were from highly inbred Strain 2, 29 from Strain 13, 23 from the F_1 generation, 47 from the F_2, 48 from backcrosses of F_1 to Strain 2, and 55 from backcrosses between F_1 and Strain 13. The animals were injected three times at monthly intervals with 100 I.U. of œstradiol benzoate and twice with 50 I.U. of œstradiol. In every case, the estradiol was followed 36 hours later with 0·2 I.U. of progesterone. The females were placed in unisexual groups, observed continuously for 14 hours, and their behavioural responses recorded. The data included individual determinations for latency and duration of heat, duration of the maximum lordosis displayed during heat and the frequency of male-like mounting. Percentage response was determined by the number of females displaying behavioural œstrus divided by the total number tested.

The results indicated that three independent genetic factors determine the character of œstrus as we have measured it. Latency of heat, duration of heat and per cent. response all show correlated inheritance and may be multiple manifestations of a single set of factors which determine the responsiveness of the individual to œstradiol benzoate. These traits display phenotypic dominance of the strain 2 values.

A completely independent genetic mechanism determines the duration of the maximum lordosis. The mode of inheritance is intermediate and the results may be interpreted in terms of a single genetic factor without dominance.

The genetic basis for male-like mounting activity appears completely independent of the genetic mechanisms for maximum lordosis. Inheritance is of the intermediate type but more than a few genetic factors are indicated and the possibility of modifiers (associated with the sex of the individual) exists.

For the female guinea pig, the pattern of behaviour displayed during œstrus is not inherited as a unitary trait. It is concluded that the negative association between mounting and duration of heat, as well as that between maximum lordosis and duration of heat, are a product of selection pressures. These associations found among the inbred strains are not attributable to genetic linkage of the traits. In addition, it is concluded that sensitivity to a hormone is genetically independent of the factors determining the quantitative character of the response.

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REFERENCES

Boling, J. L. & Blandau, R. J. (1939). The estrogen-progesterone induction of mating responses in the spayed female rat. *Endrocrinology*, **24**, 359-364.

Boling, J. L., Young, W. C. & Dempsey, E. M. (1938). Miscellaneous experiments on the estrogen-progesterone induction of heat in the spayed guinea pig. *Endocrinology*, **23**, 182-187.

Goy, R. W. & Young, W. C. (1957a). Strain differences in the behavioural responses of female guinea pigs to alpha-œstradiol benzoate and progesterone. *Behaviour*, **10**, 340-354.

Goy, R. W. & Young, W. C. (1957b). Somatic basis of sexual behaviour patterns in guinea pigs: Factors involved in the determination of the character of the soma in the female. *Psychosom. Med.*, **29**, 144-151.

Jakway, J. S. (1959). The inheritance of patterns of mating behaviour in the male guinea pig. *Anim. Behav.*, **7**, 150-162.

Lorenz, K. (1958). The evolution of behaviour. *Sci. Amer.*, **199**, 67-82.

Riss, W. (1955). Sex drive, oxygen consumption and heart rate in genetically different strains of male guinea pigs. *Amer. J. Physiol.*, **180**, 530-534.

Thompson, W. R. (1957). Traits, factors, and genes. *Eugen. Quart.*, **4**, 8-16.

Valenstein, E. S., Riss, W. & Young, W. C. (1954). Sex drive in genetically heterogeneous and highly inbred strains of male guinea pigs. *J. comp. physiol. Psychol.*, **47**, 162-165.

Young, W. C., Dempsey, E. W., Myers, H. J. & Hagquist, C. W. (1938). The ovarian condition and sexual behaviour in the female guinea pig. *Amer. J. Anat.*, **63**, 457-483.

Young, W. C. & Rundlett, B. (1939). The hormonal induction of homosexual behaviour in the spayed female guinea pig. *Psychosom. Med.*, **1**, 449-460.

Young, W. C. (1941). Observations and experiments on mating behaviour in female mammals. *Quart. Rev. Biol.*, **16**, 135-156.

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INHERITANCE OF PATTERNS OF MATING BEHAVIOUR IN THE MALE GUINEA PIG*

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Presumptive evidence for the heritable nature of patterns of mating behaviour has been gathered from the comparison of genetically different stocks of several species, in some cases genetically heterogeneous and in others highly inbred strains. Other evidence has been obtained from the testing of hybrid crosses, selective breeding, and the study of monozygous siblings.

Strains of rats having an unusually low sex drive have been found. Evans (1928) reported such a case in a highly inbred strain of albinos; other aspects of fertility were normal. Males from a strain selectively bred for high incidence of female prostate were poor breeders (Mahoney & Witschi, 1947). Females of the strain cared poorly for their litters. A pedigree-study established the hereditary nature of low libido in males of a commercial strain (Craig, Casida & Chapman, 1954). Rasmussen (1952) found that five generations of selective breeding of rats resulted in the separation of strains with high and low sex drive as measured in a modified Columbia obstruction apparatus. In the F_5 generation the males and females of the high drive strain crossed an electrified grill to reach an animal of the opposite sex approximately six times more frequently than those of the low drive strain.

Males from two inbred strains of house mice differed in mating success when a male from each strain and a single female were caged together (Levine, 1958). Another two-strain comparison in the mouse suggested hereditary differences in the relationship of sexual to aggressive behaviour (Fredericson, Story, Gurney & Butterworth, 1955).

Eriksson (1939) and Lagerlöf (1951) proposed that weak heat and indisposition to serve have a genetical basis in cattle. The latter suggestion was supported by Olson & Petersen (1951) who reported that a set of monozygous triplet bulls lacked interest in serving. Additional data came from a 7-year study of six pairs of monozygous twin bulls (Bane, 1954). Although of the same breed, the pairs came from different herds of non-inbred stock and differed considerably in genotype. Brothers were markedly alike in quantitative and qualitative aspects of mating behaviour, but there was considerable difference between the pairs. The same relationship obtained in measures of semen quantity and quality, in "temperament", and in morphological characteristics.

Studies of this sort, dealing with the rather gross patterns of behaviour, are of value in demonstrating a genetic influence, but do not contribute to our knowledge of the mode of inheritance. For this purpose more precise information is provided by the study of the *elements* or *measures* composing the patterns. The availability of two inbred strains had enabled us to investigate the inheritance of elements of the patterns of mating behaviour in the male guinea pig. Data pertaining to the genetics of reproductive behaviour in the female are presented in a companion article (Goy & Jakway, 1959).

Materials and Methods

Animals from Strains 2 and 13 were used. A complete account of the history of the strains was given by Wright (1922a) and Riss (1955). Sibling matings were made for approximately 30 generations between 1906 and 1933. Between 1933 and 1940 the stocks were maintained by within-strain matings. Following this period sibling matings were resumed at the National Cancer Institute. The sub-strains in the Kansas laboratory were obtained in 1949. Animals used in the present study were from generations F_{21} through F_{23}, after resumption of brother-sister matings in 1940, and from within-strain random matings from these generations.

These strains are believed to have an exceedingly high degree of homozygosity. As early as 1927 tissue transplants between brothers of the strains were almost as good as auto-transplants

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Table I. Sources, Designations and Procedures for Crossbred Animals

Group designation	Sire strain	Dam strain	Number of animals	Number for behavioural observations	Number autopsied
F_1 ⟩ F_1	2	13	9	9	9
F_1	13	2	11	11	7
F_2	F_1	F_1	30	30	30
$13F_1$ ⟩ B13*	13	F_1	34	34	34
$F_1 13$	F_1	13	24	24	24
$2F_1$ ⟩ B2†	2	F_1	26	26	26
$F_1 2$	F_1	2	27	27	24

*Backcross to strain 13. †Backcross to strain 2.

(Loeb & Wright, 1927). Also with respect to birth weight, adult weight, testis weight, and adrenal weight the sub-strains maintained at Kansas are remarkably similar to those studied between 1922 and 1942 (Wright, 1922a; Wright & Eaton, 1929; McPhee & Eaton, 1931; Eaton, 1938; Strandskov, 1939; Eaton, 1941; Strandskov, 1942).

One hundred and sixty-one males from the F_1 and F_2 hybrid generations, as well as backcrosses to both Strains 2 and 13 were obtained. Morphological and behavioural data were obtained as shown in Table I.

Eighteen strain 13 males and 20 strain 2 males served as controls for the behavioural observations. Because of other needs in the laboratory 8 of the Strain 13 animals could not be killed following the testing period. Additional morphological material was obtained from 11 strain 13 males, and from 3 strain 2 males. Rearing conditions for these animals were identical with those of the original experimental groups.

The animals were left with their own dams and siblings until weaning on day 25. They were then placed in individual cages 2 ft. × 2 ft. × 1 ft. with two females their own age. The caging in such groups assured each male of the contact with other animals which is necessary to bring out the behavioural differences between males of the two inbred strains (Valenstein, Riss & Young, 1955). On day 73 the female cagemates were removed.

Between the ages of 77 and 120 days each animal was observed in seven, approximately weekly, 10-minute tests with estrous females. The mean score from this number of observations is expressive of the mating performance of a given animal (Grunt & Young, 1952). Elements or measures of sexual behaviour including circling, sniffing and nibbling, nuzzling, mounting, intromissions, and ejaculations were recorded. These elements are defined as follows: *Circling* is the term employed when the male circles the female. *Sniffing and nibbling* is recorded each time the nose of the male touches the female other than in the ano-genital region. *Nuzzling* is recorded when the nose touches the ano-genital region of the female. *Mounting* is scored when the male places both forepaws on the female. *Intromission* is recorded when the penis penetrates the vaginal orifice. This is accompanied by rhythmic pelvic thrusts. *Ejaculation* is accompanied by a convulsive contraction of the haunches and terminates the display of sexual behaviour.

A test score is a numerical value reflecting three factors: the interval to ejaculation (latency of ejaculation), the amount of sexually oriented activity, and the maturity level of the behaviour (Young & Grunt, 1951; Valenstein, Riss & Young, 1954). With the exception of circling which is not scored, each measure is given a numerical value from the lowest for sniffing and nibbling to the highest for ejaculation. The value of each is then multiplied by a factor expressive of latency of ejaculation; the shorter the latency, the higher the factor. Since most tests in which ejaculation occurred were terminated before the end of the tenth minute, measurements other than scores will be expressed as rates/15 seconds.

Inasmuch as a sexual behaviour score can be attained in several ways (Young, 1957), the components were analysed separately for possible patterns of inheritance. For each element the

means for the males in each genetic group were determined. The reciprocal crosses within each group were determined separately, and then combined if they did not differ significantly. Except where nonparametric techniques are noted, the significance of differences was calculated by the *t* test, with no assumption as to equality of variances. The *t* test was also used for the comparison of groups in morphological measures and oxygen consumption.

Data obtained by Riss (1955) pointed toward a difference between males of Strains 2 and 13 in oxygen consumption. Inasmuch as oxygen consumption like sexual behaviour score is a composite measure, it was of interest to determine whether a pattern of inheritance was apparent. Between 1 and 3 days after the seventh mating test, on or about the 120th day of age, the oxygen consumption of each animal, expressed as cc 0_2/100 g. body weight/hour, was determined in the apparatus described by Peterson, Webster, Rayner & Young (1952).

In order to relate the patterns of inheritance and the amount of variation in single physical characteristics to the behavioural measures, certain morphological measurements were made. One or two days following the determination of oxygen consumption each animal was weighed and killed by a blow on the head. Both testes, the left adrenal, and the seminal vesicles were weighed. After removal of the binding connective tissue, the seminal vesicle-length from union with the ductus deferens to the tip was measured.

Adrenals from 3 strain 2, 3 strain 13, and 3 F_1 hybrid males were fixed in Bouin's fluid, sectioned at 5μ, and stained with Harris's alum hematoxylin and eosin.

Results

Circling. This measure was recorded for all groups with the exception of the F_1 animals. Circling is not specifically sexual behaviour, inasmuch as it takes place when a strange animal of either sex is placed in the home cage of another. It was felt, however, that should any pattern of inheritance appear in this measure it might profitably be compared with elements that are unequivocally mating behaviour.

As can be seen (Table II) the rate of circling in strain 2 animals far exceeded that of the strain 13 animals ($t=5{\cdot}734$, $P<{\cdot}001$). Comparison of means for all hybrid groups with those of the parent strains indicates a dominance of the slow Strain 13-type of activity. The premise is upheld

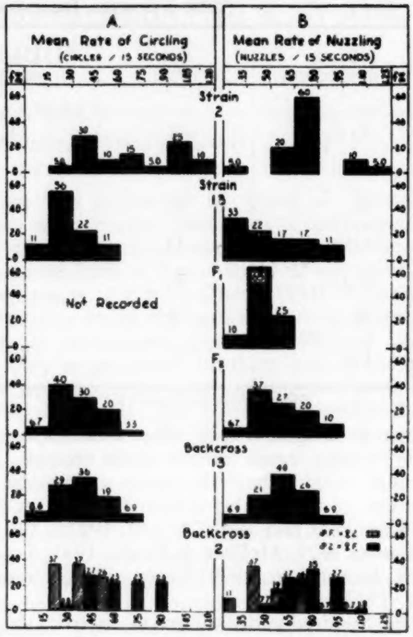

Fig. 1. Frequency distributions of behavioural measures; Rate of circling and rate of nuzzling.

by a comparison of group distributions (Fig. 1A). Because of a significant difference between means of the reciprocal B2 crosses ($P<{\cdot}001$), the use of a common group mean is not justified, consequently, $F_1 2$ and $2F_1$ groups are entered separately in Table II and Fig. 1A.

Sniffing and nibbling. Although this measure is included in the total sex score, like circling, it is not exclusively a measure of sexual behaviour.

No pattern of inheritance is apparent from a comparison of either the means or distributions of the genetic groups in rate of sniffing and nibbling. Although the rate of the strain 2 animals (1·18/15 sec.) exceeded that of the strain 13 animals (1·08/15 sec.) the difference is not significant. Neither did the inbred groups differ significantly from the F_2 animals (1·04), or from either backcross group. However, since reciprocal crosses within both backcross groups differ significantly ($2F_1=1{\cdot}28$, $F_1 2=1{\cdot}02$, $P<{\cdot}001$; $13F_1=1{\cdot}28$, $F_1 13=1{\cdot}12$, $P<{\cdot}01$), three comparisons with the inbred strains reach significance at the 5 per cent. level. Therefore, it seems safe to assume that the two inbred strains are similar with respect to physiological con-

Table II. Lower Components of Mating Behaviour
(means, standard errors, and significance of differences)

Group	N	Circling / 15 sec.			Nuzzling / 15 sec.				Mounting / 15 sec.			
		$\overline{X}$	P		$\overline{X}$	P			$\overline{X}$	P		
			2	13		2	13	F_1		2	13	F_1
Strain 2	20	·68 ± ·052		< ·001	·73 ± ·040		< ·01	< ·001	·76 ± ·039		< ·001	< ·001
Strain 13	18	·28 ± ·029	< ·001		·50 ± ·044	< ·01		*	·35 ± ·027	< ·001		< ·01
F_1	20	— —			·44 ± ·018	< ·001	*		·45 ± ·022	< ·001	< ·01	
F_2	30	·36 ± ·027	< ·001	*	·57 ± ·027	< ·01	*	< ·001	·47 ± ·022	< ·001	< ·01	*
B_{13}	58	·36 ± ·020	< ·001	< ·05	·59 ± ·019	< ·01	*	< ·001	·35 ± ·017	< ·001	*	< ·01
F_1♂x13♀	24											
13♂xF_1♀	34											
B_2	53								·63 ± ·027	< ·02	< ·001	< ·001
F_1♂x2♀	27	·37 ± ·024	< ·001	< ·05	·58 ± ·034	< ·01	*	< ·01				
2♂xF_1♀	26	·58 ± ·034	*	< ·001	·72 ± ·028	*	< ·001	< ·001				

* = P > ·05

ditions underlying the performance rate of this form of activity and that no change of modifying factors by recombination in hybrid generations is likely to decrease or enhance the rate.

Nuzzling. Again the strain 2 animals exceeded those of Strain 13 in rate of activity. The difference reaches significance at the 1 per cent. level. Means, standard errors, and comparison of all genetic groups with the pure strains and F_1 hybrids are given in Table II. For this measure the means and distributions (Fig. 1B) of the genetic groups strongly suggest a dominance in inheritance of the sluggish strain 13 pattern. A significant (P<·01) difference between reciprocal backcrosses to Strain 2 animals cannot be explained.

Mounting. The pattern of inheritance is clearer than that for any of the preceding measures. Strain 2 males (0·76 mounts/15 sec.) greatly exceeded those of Strain 13 (0·35 mounts/15 sec.) in the measure. In this case there are no real differences between reciprocals in either backcross group. Comparison of the means (Table II) shows that, although intermediate between the two pure strains, the values for the F_1 and F_2 hybrids fall well below the mid-parent mean of 0·55. This, as well as the extended range of the B_2 animals (Fig. 2A), and the similarity of the B_{13} animals to the distribution of their pure strain parents, suggests a dominance of the lethargic Strain 13 pattern.

It can be generalised that for the inheritance of the individual components of mating behaviour

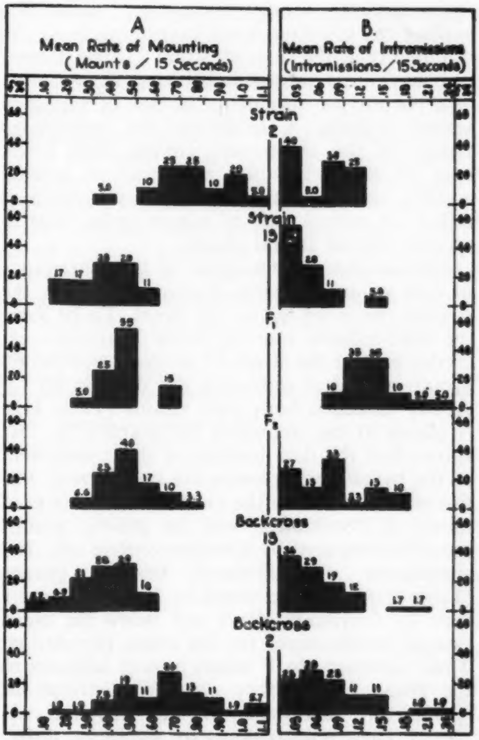

Fig. 2. Frequency distributions of behavioural measures; Rate of mounting and rate of intromission.

Table III. Higher Components of Mating Behaviour
(means, standard errors, and significance of differences)

Group	N	Intromissions / 15 sec. $\bar{X}$	P 2	P 13	P F_1	Number of ejaculations in seven tests $\bar{X}$	P 2	P 13	P F_1
Strain 2	20	·056±·0092		<·02	<·01	1·10		*	<·001
Strain 13	18	·038±·0089	<·02		<·001	0·61	*		<·001
F_1	20	·136±·0078	<·01	<·001		4·85	<·001	<·001	
F_2	30	·079±·0091	*	<·01	<·01	1·47	*	*	<·001
B_{13}	58	·056±·0053	*	*	<·001	1·14	*	*	<·001
B_2	53	·070±·0071	*	<·05	<·001				
F_1♂ x 2♀	27					2·48	<·02	<·001	<·001
2♂ x F_1♀	26					0·85	*	*	<·001

* = P>·05

from circling through mounting, except for sniffing and nibbling, a mechanism involving the dominance of the sluggish strain 13-type pattern of behaviour is indicated. This may be expressed as a phenotypic dominance of lack of vigour in sexual activity. Considering the ambiguous nature of the component circling with reference to characterisation as sexual or general activity, the dominantly heritable lethargy may reflect an overall lack of vigour rather than a specific lack of sexual vigour.

Intromission. Examination of the inheritance of rate of intromission reveals a break in the pattern presented up to this point. To be sure, the intromission rate of strain 2 animals exceeded that of the strain 13 animals, but the F_1 group, instead of mirroring the slow Strain 13, greatly exceeded both pure strains (Table III). A glance at the frequency bar graph (Fig. 2B) shows that the distributions of this component of the behavioural pattern are not normal. For this reason the use of the *t* test for comparison of means is invalidated, and the genetic groups must be compared by a nonparametric test. The significance of differences between groups (Table III) were determined by 2 × 2 chi square tests for frequency above and below the mean rate of intromissions for the entire population. Thus, although the P values appear adjacent to the group means, they compare distributions (graphically represented in Fig. 2B) and not means. There is no evidence for significant differences between any of the reciprocal crosses. The high rate of intromissions characteristic of the F_2 group may represent residual heterosis. However, the high values for both backcross groups indicate phenotypic dominance of the strain 2 pattern.

Number of ejaculations. In view of the large number of animals which did not achieve ejaculation within any 10-minute observation period (Fig. 3A), the distributions of the "number of ejaculations in seven tests" are far from normal. Consequently, it was necessary to employ a test for significance of differences between groups not based on an assumption of normality. As such, the Mann-Whitney U statistic for nonparametric data, corrected for ties, was used (Siegel, 1956). Analysis of the measure demonstrates that, despite a general lack of vigour in terms of activity rate, the F_1 group exhibited a readiness to ejaculate which exceeded that in its pure strain progenitors (Table III, Fig. 3A). The distribution of the F_2 group indicates some degree of residual heterosis. The difference between the two reciprocal crosses in the B_2 group (P=·002) is inexplicable in terms of the present data. There is a possibility that this sample of Strain 2 controls was abnormally low in frequency of ejaculation. In 1955, 19 similarly reared males of the strain were found to have a mean number of ejaculations of 3·7 in seven tests (Valenstein, Riss & Young, 1955). It seems possible that the strain 2 backcross animals may be indicative of the actual range of the Strain 2 population and may

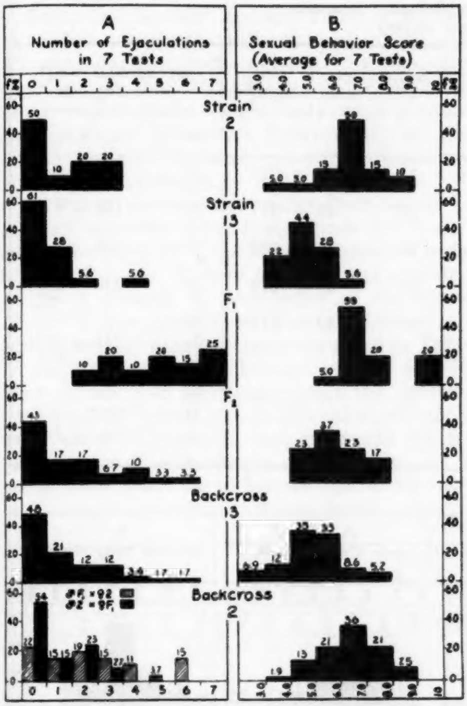

Fig. 3. Frequency distribution of behavioural measures; Ejaculation frequency and sexual behaviour score.

thus exceed the range of the present control sample. In 1955 seven males from Strain 13 achieved a mean of 0·6 ejaculations in seven tests, which is identical with the present sample of that strain.

Sexual behaviour score. We have seen that the elements of the mating pattern have two distinctly different modes of inheritance. Knowing this, it is of interest to examine the mode of inheritance of the composite trait, the sexual behaviour score. There was no instance of a significant difference between any of the reciprocal crosses. The mean score and standard error of the mean for each group are presented in Table IV, with the P value for comparison of each group with the two inbred strains and the F_1 hybrids. The means suggest dominance of the higher scoring strain 2 males with a heterotic increase in the F_1 generation. Examination of the frequency bar graph (Fig. 3B), however, create doubt as to the simplicity of the mechanism. The ranges of the two backcross groups are more suggestive of an intermediate type of inheritance than of a pattern of simple dominance. The ambiguous nature of the mode of inheritance of the total score bears out the prediction based on a separate analysis of its component elements.

Oxygen Consumption

Oxygen consumption in the two strains was not significantly different. In earlier studies Riss (1955) and Riss & Goy (1957), using the same apparatus, demonstrated a tendency for higher oxygen consumption among strain 2 than among strain 13 males. Readings from the greater number of animals employed in the present study indicate the same trend, but do not establish statistical significance for the difference (Table V). Assuming that the tendency is valid, the

Table IV. Mating Behaviour Score
(mean, standard error, and significance of differences).

Group	N	Sexual behaviour score			
		$\bar{X}$	P		
			2	13	F_1
Strain 2	20	6·4 ± ·23		< ·001	< ·02
Strain 13	18	4·6 ± ·19	< ·001		< ·001
F_1	20	7·3 ± ·25	< ·02	< ·001	
F_2	30	5·7 ± ·18	< ·05	< ·001	< ·001
B_{13}	58	4·9 ± ·15	< ·001	*	< ·001
B_2	53	6·2 ± ·17	*	< ·001	< ·01

* = P > ·05

Table V. Physiological and Morphological Measures
(means and standard errors)

Group	O_2 consumption cc/hr/g.		Body weight at at 120 days		Seminal vesicle weight (% of body weight)		Left adrenal weight in milligrams	
	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$
Strain 2	23	$65{\cdot}4 \pm 1{\cdot}29$	23	$611{\cdot}7 \pm 18{\cdot}69$	22	$\cdot38 \pm \cdot021$	22	$241 \pm 6{\cdot}5$
Strain 13	18	$62{\cdot}3 \pm 1{\cdot}21$	28	$776{\cdot}8 \pm 18{\cdot}21$	20	$\cdot48 \pm \cdot017$	21	$196 \pm 5{\cdot}0$
F_1	20	$64{\cdot}2 \pm 1{\cdot}08$	20	$748{\cdot}8 \pm 16{\cdot}26$	16	$\cdot46 \pm \cdot020$	16	$244 \pm 4{\cdot}0$
F_2	30	$64{\cdot}4 \pm 0{\cdot}84$	30	$729{\cdot}7 \pm 17{\cdot}41$	29	$\cdot47 \pm \cdot019$	30	$230 \pm 4{\cdot}4$
B_{13}	58	$60{\cdot}7 \pm 0{\cdot}79$	58		58	$\cdot50 \pm \cdot011$	58	
F_1♂x13♀			24	$783{\cdot}8 \pm 15{\cdot}90$			24	$211 \pm 4{\cdot}5$
13♂xF_1♀			34	$835{\cdot}7 \pm 10{\cdot}18$			34	$192 \pm 2{\cdot}9$
B_2	53	$64{\cdot}0 \pm 0{\cdot}84$	53	$672{\cdot}8 \pm 12{\cdot}72$	50	$\cdot43 \pm \cdot010$	50	
F_1♂x2♀			27	$668{\cdot}4 \pm 15{\cdot}97$			24	$227 \pm 4{\cdot}9$
2♂xF_1♀			26	$677{\cdot}5 \pm 20{\cdot}24$			26	$203 \pm 5{\cdot}7$

frequency distributions (Fig. 4A) suggest an intermediate type of inheritance.

Morphological Measurements

Body weight. Males of Strain 13 are heavier than those of Strain 2. The difference has persisted as a fixed trait since at least 1922 (Wright, 1922a; Wright & Eaton, 1929; Eaton, 1938, 1941; Strandskov, 1939). Although the weights of neither the reciprocal F_1 hybrids nor reciprocals in the B_2 group differ significantly, there is a real difference between the reciprocals in the B_{13} group. A comparison of the means (Table V) suggests a dominance of the heavy strain 13 type. This suggestion is strengthened by the frequency distributions (Fig. 4B) which demonstrate (1) the similarity in range of the B_{13} group and of the pure Strain 13, and (2) the recovery by the B_2 animals of all but the extreme pure strain classes,

The progeny of the vigorous F_1 dams maintained a greater weight up to the 120th day of age when the experiment was terminated. Within the backcross groups both crosses of F_1 maternity exceeded their reciprocal crosses. In B_{13}, with the genetic background for large size, the mean of the $13F_1$ group exceeded, not only its recriprocal cross ($P<{\cdot}02$), but also the pure strain 13 males ($P<{\cdot}01$). In addition the high mean weight of the F_2 generation suggests the operation of a maternal factor. Although within the B_2 group the $2F_1$ group exceeded the F_12 in adult body weight, the difference is not significant.

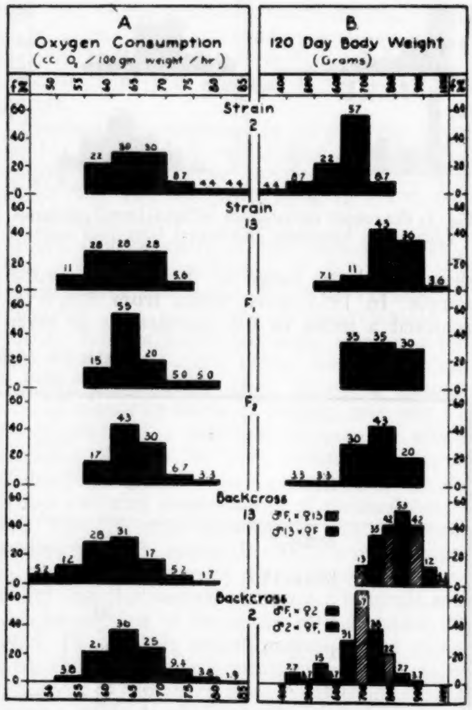

Fig. 4. Frequency distributions of physiological and morphological measures; oxygen consumption and body weight.

Testes and seminal vesicles. There is no evidence for a separate mechanism of inheritance for testicular and body weights. The two vary together, so that comparison of the adjusted testis weights (testis weight/body weight) yields no significant differences between any of the genetic groups. The same condition obtains for seminal vesicle length.

In weight the seminal vesicles from Strain 13 animals exceeded those from Strain 2 animals, both absolutely ($P < \cdot 001$) and adjusted to body weight ($P < \cdot 01$). In both absolute and adjusted weight a pattern of dominance of the heavy Strain 13 type is followed. Group means of adjusted seminal vesicle weights are given in Table V and frequency distributions in Fig. 5A. In both actual and adjusted weight the seminal vesicles of all hybrid groups differed significantly from those of Strain 2, and none but the B_2 group differed significantly from strain 13. It seems most plausible to assume that along with testis weight and seminal vesicle length, seminal

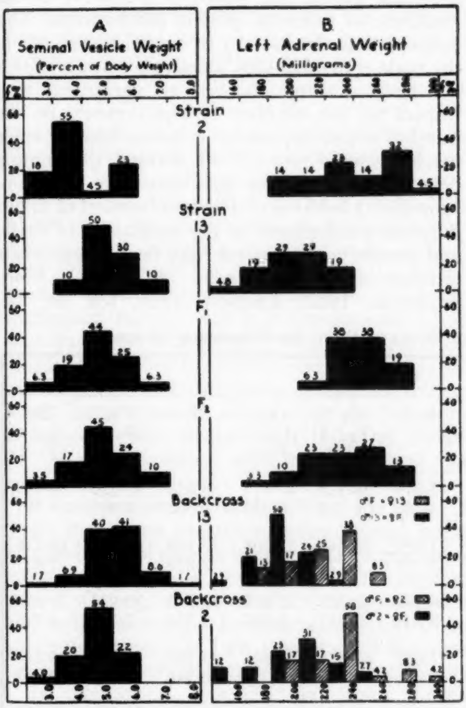

Fig. 5. Frequency distributions of morphological measures; weights of seminal vesicle and adrenal.

vesicle weight is a reflection of the size of the animal.

Adrenal gland. Unlike the other measurements, the mean absolute weight of the adrenal glands of the strain 2 animals far exceeded that of the strain 13 animals ($P < \cdot 001$) (Table V). This relationship was noted by Eaton in 1938 and Strandskov in 1939, so apparently was fixed in the strains before that time. Inasmuch as strain 2 animals are smaller, adjustment for body weight magnifies the strain difference and use of adjusted adrenal weights in a genetic analysis is invalid. A comparison of means shows that in absolute weight the adrenals from the F_1 and the F_2 animals did not differ significantly from those from the strain 2 animals (Table V). When compared with the pure strains the mean adrenal weights of the F_1 and F_2 generations suggest a dominance in inheritance of the large strain 2-type adrenal which is transmitted independently of body size. Mean adrenal weights from the reciprocal crosses within the B_{13} group differed significantly ($P < \cdot 01$) as did the reciprocal crosses within the B_2 group ($P < \cdot 01$). Within both backcross groups the animals of F_1 maternity had the smaller adrenals. The apparent simplicity in inheritance of the F_1 and F_2, and the profound difference between the reciprocal backcross groups is demonstrated in Fig. 5B).

The independent inheritance of adrenal and body weight is also demonstrated by within-group correlations between the two statistics. The weight of the strain 2 adrenals is positively correlated with the weight of the bodies ($r = \cdot 727$, $P < \cdot 01$) while within strain 13 the adrenal-body weight correlation is not significant ($r = \cdot 391$, $P < \cdot 1$). The correlation is strong in the F_1 generation ($r = \cdot 718$, $P < \cdot 01$), but not in the F_2 generation ($r = \cdot 166$, $P < \cdot 5$). This again suggests a dominance of the strain 2-type adrenal, with independent segregation of adrenal-type and body-type in the F_2 generation. Within each of the reciprocal strain 2 backcross groups the correlation is significant ($2F_1$, $r = \cdot 777$, $P < \cdot 01$; $F_1 2$, $r = \cdot 474$, $P < \cdot 02$) as it is in the group as a whole ($r = \cdot 582$, $P < \cdot 01$). On the other hand, while the correlation is positive in each of the reciprocal strain 13 backcross groups ($13F_1$, $r = \cdot 448$, $P < \cdot 01$; $F_1 13$, $r = \cdot 439$, $P < \cdot 05$), it is not significant when the group is taken in its entirety ($4 = \cdot 215$, $P < \cdot 1$).

When the adrenals from the pure strain and the F_1 animals were studied microscopically the medulla appeared to be about the same quantitatively and qualitatively in the three groups.

On the other hand, the cortices from animals of the two pure strains were strikingly different. The cross sectional diameters in the strain 2 adrenals were greater. The differences can be ascribed in large part to the much greater number of cytoplasmic vacuoles in the cells of the zona fasciculata of the strain 2 adrenals. Such vascuoles were extremely sparse in the strain 13 glands. From the few F_1 adrenals available it is evident that the cytoplasm is vacuolated to a considerably greater degree than in the strain 13 adrenals. One other case of heritable difference in adrenal cortex structure has been reported. In a study of F_1, F_2, and backcross hybrids of two strains of mice in which the lipid content of the adrenal cortex differed, Arnesen (1955) found a dominance of the high-lipid type.

Coefficients of Variation

The coefficients of variation (V) for each group were determined by 100 δ/mean. The standard error of V, or δv is $V\sqrt{2N}$ when V is less than 15, and $(V/\sqrt{2N})\ (1 + 2\ [V/100]^2)$ when V is greater than 15. This statistic is not influenced by population size or size of the mean, and enables us to compare the variation in each measure within the groups.

In the four behavioural measures for which data are available (nuzzling, mounting, intromissions, score) the coefficients of variation of the F_1 generation are less than those of either pure strain (Table VI). The same relationship holds for oxygen consumption and the three morphological measures, body weight, seminal vesicle weight, and adrenal weight (Table VII). The value rises from the F_1 to the F_2 generation for all behavioural and morphological measures. Only for oxygen consumption is the coefficient of variation somewhat lower for the F_2 group than for the F_1 group. The coefficient of variation tends to rise still further in the backcross generations.

In general then variation decreased in the genetically homogeneous F_1 animals and increased as segregation and recombination occurred in the later hybrid generations. Graphic substantiation is given by the entire set of frequency distributions (Figs. 1-5).

Discussion

A number of generalisations bear (1) on theory dealing with the physiology of mating behaviour in the male, and (2) on an extension of the study of inheritance of structural characteristics to the study of behavioural traits.

It is clear first that there is a duality in the manner of inheritance of the lower and higher elements of the pattern of mating behaviour in the male guinea pig which is indicative of the existence of different genetic mechanisms. The concept that the pattern of sexual behaviour in the male is divided into separable components is not new, although there is no agreement with respect to the number of components or the number whose expression is controlled by single mechanisms. Craig (1918) divided the mating behaviour of pigeons into appetitive and consummatory behaviour. The involvement of differdifferent mechanisms in the mediation of these, and possibly other parts, has been suggested a number of times (Beach, 1942, 1947, 1948; Soulairac, 1952; Larsson, 1956, for the rat;

Table VI. Coefficients of Variation (V) and Standard Errors of V (δv) for Behavioural Measures

		Group									
		Strain 2	Strain 13	F_1	F_2	B_{13}	F_1 13 (F_1♂ x 13♀)	13F (13♂ x F_1♀)	B_2	$F_1$2 (F_2♂ x 2♀)	2F_1 (2♂ x F_1♀)
Circling	V	34·438	44·207	—	41·816	43·819	38·323	47·473	38·828	33·220	30·447
	δv	6·056	8·689	—	6·272	4·786	6·292	6·934	4·302	4·995	4·597
Nuzzling	V	24·344	37·654	18·172	26·005	23·979	26·743	22·266	27·149	30·927	19·710
	δv	4·071	7·110	2·967	3·577	2·351	4·127	2·831	2·824	4·593	2·837
Mounting	V	22·916	33·303	22·098	25·010	36·470	42·359	32·497	31·373	30·923	31·305
	δv	3·809	6·131	3·661	3·425	3·810	7·127	4·337	3·334	3·108	4·748
Intromissions	V	73·863	99·499	25·777	63·409	71·678	81·874	60·926	73·262	51·398	98·586
	δv	16·882	28·627	4·338	10·996	9·476	18·080	9·752	10·246	8·647	23·457
Score	V	15·846	18·064	15·167	17·454	23·594	27·825	20·306	19·377	20·591	17·908
	δv	2·567	3·107	2·425	2·321	2·309	4·316	2·562	1·951	2·918	2·562

Table VII. Coefficients of Variation (V) and Standard Errors of V (δv) for Oxygen Consumption and Morphological Measures.

		Group									
		Strain 2	Strain 13	F_1	F_2	B_{13}	$F_1 13$ (F_1♂ x 13♀)	13F (13♂ x F_1♀)	B_2	$F_1 2$ (F_1♂ x 2♀)	$2F_1$ (2♂ x F_1♀)
Oxygen consumption	V	9·439	8·242	7·538	7·114	9·926	9·311	10·251	10·611	9·212	10·020
	δv	1·392	1·374	1·192	0·918	0·922	1·344	1·243	0·933	1·254	1·389
Body weight	V	14·658	12·409	9·712	13·104	8·819	9·937	7·112	13·769	12·419	15·232
	δv	2·161	1·659	1·536	1·692	0·819	1·434	0·862	1·337	1·690	2·161
Seminal vesicles	V	27·495	22·160	15·499	22·845	18·986	21·001	17·755	21·404	15·360	26·227
	δv	4·664	3·583	2·805	3·152	1·825	3·162	2·220	2·236	2·269	3·879
Adrenal weight	V	12·669	11·633	6·656	10·505	10·602	10·550	8·764	13·534	14·250	10·506
	δv	1·910	1·795	1·177	1·356	0·984	1·523	1·063	1·353	1·976	1·516

Rosenblatt & Aronson, 1958, for the cat; Clark, Aronson & Gordon, 1954; Baerends, Brouwer & Waterbolk, 1955, for several fishes). Soulairac and Larsson considered that the mechanism for the activity culminating in intromission differed from that mediating ejaculation. The inference from the present study is that the break may lie between mounting and intromission.

No hint is given as to the nature of the physical factor or factors underlying the increased readiness of the F_1 hybrids to ejaculate. While the F_1 hybrids combined the large body size of Strain 13, with heavy adrenal typical of Strain 2, the same combination existed in the F_2 hybrids in which there was no increase in ejaculation frequency. It is probable that in the F_1 hybrids readiness to ejaculate is not associated with a chance combination of favourable, randomly segregated factors, but is a consequence of an undefined heterotic vigour. Such heterosis in the mating behaviour of male guinea pigs was noted by Wright (1922b) following crosses, not only of strain 2 and strain 13 animals, but also following crosses of these strains with those of Strains 32, 35, and 39 which were in existence at that time.

It has become evident during the past 20 years that some variation within animal populations is not of genetic origin. (1) The amount of variation within a genetically homogeneous group of one genotype need not be equivalent to that within an equally homogeneous group of another genotype. (2) Two groups with the same genotypic constitution may differ phenotypically.

In connection with the first point, Lerner (1954) has cited studies showing that F_1 heterozygotes tend to show less variation than the inbred strains from which they are derived, although both the inbred and F_1 groups are genetically homogeneous. Additional evidence has come from studies of growth in chickens (Clough & Cock, 1957), cranial measurements (Bader, 1956), the composition of liver mitochondria in mice (Caspari, 1956), wing length, thorax length, the per cent. of emergence of fruit flies (Tantawy, 1957), vaginal response of mice to estrogens (Claringbold & Biggers, 1955), and the response of mice to Nembutal (McLaren & Michie, 1956). The extension of this phenomenon from the realms of morphology and physiology to that of behaviour, as demonstrated in the present study, is new. Lerner has advanced the hypothesis that an F_1, heterozygotic, animal is capable of greater stability in dealing with environmental fluctuations than is the more variable homozygous animal; that while a homozygous animal may be less stable in the face of environmental change, a heterozygous animal will tend to be buffered against such variation. In the present study elements of sexual behaviour may be thought of as measures of the response of the male to the estrous female; variations to the same stimulus object, therefore, would be greater in the homozygous males, as indeed it was.

Differences between groups having the same genetic constitution have been found. Castle, Gates, Reed & Law (1936) and Chai (1956) showed that when large and small races of mice were crossed, progeny of the large mothers were heavier than progeny from the reciprocal cross. Walton & Hammond (1938) demonstrated that in Shire horse-Shetland pony crosses colts from the Shire horse mares were larger than those

from Shetland mares. Maternal age has been demonstrated to be responsible for an increased penetrance of the "eyelids open" defect in genetically homogeneous mice (Hauschka & Brown, 1954), and for the increased percentage of white spotting (Wright, 1926) and polydactyly (Wright, 1934) in highly inbred guinea pigs. The presence of a tooth anomaly in members of a strain of inbred mice was shown by Grüneberg (1951) to be the result of physiological conditions of the mother acting on litters as a whole. In our data there were several instances in both behavioural and morphological measures of significant differences between reciprocal groups within hybrid generations. These differences occurred in the two backcross generations (B_{13} and B_2) but not in reciprocal F_1 groups. Backcross progeny from F_1 females were heavier than progeny from females of either inbred strain. They also achieved higher scores in several of the lower activity measures (circling, sniffing and nibbling, and nuzzling). On the other hand, number of ejaculations and adrenal weight were highest in progeny of inbred dams.

Summary

The manner of inheritance of the sexual behaviour pattern of the male guinea pig has been studied. A separate analysis was made of each component of the behavioural pattern; circling, sniffing and nibbling, nuzzling, mounting, intromission, and ejaculation. Animals from the inbred strains 2 and 13, as well as from the F_1 and F_2 hybrid generations and from backcrosses to both strains were used. As a young adult, each animal was scored in seven weekly 10-minute observations with an œstrous female. Measurements of body weight, testis weight, seminal vesicle length and weight, adrenal weight, and oxygen consumption were made for each animal at approximately 120 days of age.

1. Genetic analysis disclosed a dominance of the lethargic strain 13-type behaviour pattern in rates of the lower measures of activity (circling, nuzzling, and mounting). Although the pattern of inheritance of the higher measures (intromission rate and number of ejaculations) was obscured by a heterotic increase in the F_1 generation, a dominance of the higher scoring strain 2-type of behaviour was suggested for both measures. The separation of the manner of inheritance of ejaculation frequency and rate of intromission, on the one hand, from the rate of performance of the lower components of the mating pattern on the other, points toward different underlying mechanisms.

2. An intermediate type of inheritance is suggested for rate of oxygen consumption. The heavier strain 13 body type showed phenotypic dominance. Testis weight, seminal vesicle weight and length appeared to follow body weight in pattern of inheritance. Adrenal glands from the strain 2 animals were heavier than those from the strain 13 animals and had a considerably higher degree of vacuolization in the cells of the zona fasciculata. Genetical analysis suggests dominance of the heavy strain 2-type gland.

3. There were several instances of significance differences between reciprocally crossed groups of the same genetic constitution. In the backcross generations progeny of F_1 dams were heavier and scored higher in several of the lower elements of mating behaviour, while progeny of inbred dams had heavier adrenals and ejaculated more frequently. This latter fact does not support hypothesis that heavy adrenals are associated with high frequency of ejaculation, for heavy adrenals were also found in F_2 hybrids in which ejaculation frequency was relatively low.

4. In both morphological and behavioural measures the coefficients of variation for the F_1 hybrids were less than those for animals in either pure strain.

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REFERENCES

Arnesen, K. (1955). Constitutional differences in lipid content of adrenals in two strains of mice and their hybrids. *Acta endocr.*, **18**, 396-401.

Bader, R. S. (1956). Variability in wild and inbred mammalian populations. *Quart. J. Fla. Acad. Sci.*, **19**, 14-34.

Baerends, G. P., Brouwer, R. & Waterbolk, H. Tj. (1955). Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courtship pattern. *Behaviour*, **8**, 249-334.

Bane, A. (1954). Studies on monozygous cattle twins. Sexual functions of bulls in relation to heredity, rearing intensity and somatic conditions. *Acta agric. scand.*, **4**, 95-208.

Beach, F. A. (1942). Analysis of factors involved in the arousal, maintenance and manifestation of sexual excitement in male animals. *Psychosom. Med.*, **4**, 173-198.

Beach, F. A. (1947). A review of physiological and psychological studies of sexual behaviour in mammals. *Physiol. Rev.*, **27**, 240-307.

Beach, F. A. (1948). *Hormones and behaviour*. New York: Hoeber, 368 pp.

Caspari, E. (1956). The inheritance of the difference in the composition of the liver mitochondria between two mouse strains. *Genetics*, **41**, 107-117.

Castle, W. E., Gates, W. H., Reed, S. C. & Law, L. W. (1936). Studies of a size cross in mice, II. *Genetics*, **21**, 310-323.

Chai, C. K. (1956). Analysis of quantitative inheritance of body size in mice. I. Hybridization and maternal influence. *Genetics*, **41**, 157-164.

Claringbold, P. J. & Biggers, J. D. (1955). The response of inbred mice to oestrogens. *J. Endocr.*, **12**, 9-14.

Clark, E., Aronson, L. R. & Gordon, M. (1954). Mating behaviour patterns in two sympatric species of xiphophorin fishes: their inheritance and significance in sexual isolation. *Bull. Amer. Mus. Nat. Hist.*, **103**, 135-226.

Clough, M. & Cock, A. G. (1957). Variability of inbred and incross chickens. *Nature (Lond.)*, **179**, 1030-1031.

Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biol. Bull., Wood's Hole*, **34**, 91-107.

Craig, J. V., Casida, L. E. &. Chapman, A. B. (1954). Male infertility associated with lack of libido in the rat. *Amer. Nat.*, **88**, 365-372.

Eaton, O. N. (1938). Weights and measurements of the parts and organs of mature inbred and crossbred guinea pigs. *Amer. J. Anat.*, **63**, 273-295.

Eaton, O. N. (1941). Effect of crossing inbred lines of guinea pigs. *Tech, Bull. U.S. Dep. Agric.*, **765**, 1-19.

Eriksson, K. (1939). Ärftlighetsondersöknongar över sterilitet hos nökreatur. (Genetical studies on sterility in cattle) 5 Nord. Veterinaermøde (Kbh.). Abstract: *Anim. breed. Anstr.*, **11**, 159. 1943.

Evans, H. M. (1928). Sterility in inbred rats. *Amer. J. Physiol.*, **85**, 154-157.

Fredericson, E., Story, A. W., Gurney, N. L. & Butterworth, K. (1955). The relationship between heredity, sex, and aggression in two inbred mouse strains. *J. Genet. Psychol.*, **87**, 121-130.

Goy, R. W. & Jakway, J.S. (1959). Inheritance of patterns of mating behaviour in the female guinea pig. *Anim. Behav.*, **7**, 142-149.

Grüneberg, H. (1951). The genetics of a tooth defect in the mouse. *Proc. roy. Soc. B.*, **138**, 437-451.

Grunt, J. A. & Young, W. C. (1952). Differential reactivity of individuals and the response of the male guinea pig to testostereone propionate. *Endocrinology*, **51**, 237-248.

Hauschka, T. S. & Brown, E. (1954). Influence of maternal age on penetrance of "eyelids open" in newborn mice. *Ann. New York Acad. Sci.*, **57**, 465-475.

Lagerlöf, N. (1951). Hereditary forms of sterility in Swedish cattle breeds. *Fertil. Steril.*, **2**, 230-242.

Larsson, K. (1956). Conditioning and sexual behaviour in the male albino rat. *Acta psychol. Goth.*, **1**, 269 pp.

Lerner, I. M. (1954). *Genetic homeostasis*. New York: Wiley, 134 pp.

Levine, L. (1958). Studies on sexual selection in mice. I. Reproductive competition between albino and black-agouti males. *Amer. Nat.*, **92**, 21-26.

Loeb, L. & Wright, S. (1927). Transplantation and individuality differentials in inbred families of guinea-pigs. *Amer. J. Path.*, **3**, 251-283.

Mahoney, J. J. & Witschi, E. (1947). Genetics of the female prostate in rats. *Genetics*, **32**, 369-378.

McLaren, A. & Michie, D. (1956). Variability of response in experimental animals. A comparison of the reactions of inbred, F_1 hybrid and random bred mice to a narcotic drug. *J. Genet.*, **54**, 440-455.

McPhee, H. C. & Eaton, O. N. (1931). Genetic growth differentiation in guinea pigs. *Tech. Bull. U.S. Dept. Agric.*, **222**, 1-36.

Olson, H. H. & Petersen, W. E. (1951). Uniformity of semen production and behaviour in monozygous triplet bulls. *J. dairy Sci.*, **34**, 489-490.

Peterson, R. R., Webster, R. C., Rayner, B. & Young, W. C. (1952). The thyroid and reproductive performance in the adult female guinea pig. *Endocrinology*, **51**, 504-518.

Rasmussen, E. W. (1952). The relation between strength of sexual drive and fertility as evident from experimental investigations. *Proc. 2nd Int. Congr. anim. Reprod., (Copenhagen)*, **1**, 188-191.

Riss, W. (1955). Sex drive, oxygen consumption and heart rate in genetically different strains of male guinea pigs. *Amer. J. Physiol.*, **180**, 530-534.

Riss, W. & Goy, R. W. (1957). Modification of sex drive and 0_2 consumption by isolating and grouping male guinea pigs. *J. comp. physiol. Psychol.*, **50**, 150-154.

Rosenblatt, J. S. & Aronson, L. R. (1958). The decline of sexual behaviour in male cats after castration with special reference to the role of prior sexual experience. *Behaviour*, **12**, 285-338.

Siegel, S. (1956). *Nonparametric statistics for the bebehavioral sciences*. New York: McGraw-Hill. 312 pp.

Soulairac, A. (1952). Étude experimentale due comportement sexual male. Independence relative des divers éléments moteurs chez le rat male normal. *Ann. Endocr. (Paris)*, **13**, 775-780.

Strandskov, H. H. (1939). Inheritance of internal organ differences in guinea pigs. *Genetics*, **24**, 722-727.

Strandskov, H. H. (1942). Skeletal variations in guinea pigs and their inheritance. *J. Mammal.*, **23**, 65-75.

Tantawy, A. O. (1957). Heterosis and genetic variance in hybrids between inbred lines of *Drosophila melanogaster* in relation to the level of homozygosity. *Genetics*, **42**, 535-543.

Valenstein, E. S., Riss, W. & Young, W. C. (1954). Sex drive in genetically heterogeneous and highly inbred strains of male guinea pigs. *J. comp. physiol. Psychól.*, **47**, 162-165.

Valenstein, E. S., Riss, W. & Young, W. C. (1955). Experiential and genetic factors in the organization of sexual behaviour in male guinea pigs. *J. comp. physiol. Psychol.*, **48**, 397-403.

Walton, A. & Hammond, J. (1938). The maternal effects on growth and conformation in Shire horse-Shetland pony crosses. *Proc. roy. Soc. B*, **125**, 311-335.

Wright, S. (1922a). The effects of inbreeding and crossbreeding on guinea pigs. I. Decline in vigour. II. Differentiation among inbred families. *Bull. U.S. Dept. Agric.*, **1090**, 1-63.

Wright, S. (1922b). The effects of inbreeding and crossbreeding on guinea pigs. III. Crosses between highly inbred families. *Bull. U.S. Dept. Agric.*, **1121**, 1-60.

Wright, S. (1926). Effects of age of parents on characteristics of the guinea pig. *Amer. Nat.*, **60,** 552-559.

Wright, S. (1934). An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics*, **19,** 506-536.

Wright, S. & Eaton, O. N. (1929). The persistence of differentiation among inbred families of guinea pigs. *Tech. Bull. U.S. Dept. Agric.*, **103,** 1-45.

Young, W. C. (1957). Genetic and psychological determinants of sexual behaviour patterns. In *Hormones, brain function and behaviour*. (Ed., Hudson Hoagland). New York: Academic Press. pp. 75-98.

Young, W. C. & Grunt, J. A. (1951). The pattern and measurement of sexual behaviour in the male guinea pig. *J. comp. physiol. Psychol.*, **44,** 492-500.

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MOTHER-YOUNG RELATIONS AND THE MATURATION OF PUP BEHAVIOUR IN THE ALASKA FUR SEAL

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The relation between mother and infant is an active field of research in animal behaviour, but in mammals most of the observations on this critical relationship have been made on captive or domestic animals living under artificial conditions and dependent at least in part on human beings for maintenance and care. In the case of domestic species, moreover, prolonged and intensive selection of individuals for convenience of domestication may have obscured or altered the nature of the interactions between parent and offspring. Opportunities to make prolonged observations on significant numbers of undisturbed, individually identifiable wild mammals are extremely scarce. The Alaska fur seal (*Callorhinus ursinus*), however, affords precisely such opportunities. During a few weeks each summer hundreds of thousands of females bear their young, come into heat, are fertilised, and perform their parental activities in a few rookeries in the Pribilof and Komandorskie Islands. From a single vantage point it is possible, without disturbing the seals, to observe scores of births, thousands of contacts between adults and young, and the gradual changes in behaviour shown by hundreds of young. In addition, the relationship of parent and offspring in this species is of particular interest because of its intermittent nature and the complex social system within which it occurs.

The Alaska fur seal has been more extensively studied than any other marine mammal and the general outlines of its life history are available in many publications. The brief summary below is taken from Bartholomew & Hoel (1953).

"During fall, winter, and early spring the animals are strictly pelagic; the females and young scatter widely over the north Pacific Ocean; the adult males remain in the vicinity of the Behring Sea and Aleutian Islands. In late spring the adult males (harem bulls) come ashore on the Pribilof Islands, establish territories spaced more or less evenly over the rookeries, and await the coming of the females (cows). The pregnant females and the young non-breeding males (bachelors) start coming ashore in the middle of June and continue to do so through July and early August. The cows are apportioned among the harem bulls. Most of the non-breeding males station themselves inland from the breeding animals. Within a few days after their arrival the females bear their pups and come into heat shortly thereafter. After mating they spend the rest of the summer feeding themselves at sea and nursing their pups on land. During the entire breeding season, which lasts approximately two months, the harem bulls stay in their territories without eating or drinking, but the sub-adult non-breeding males go to sea at irregular intervals. Toward the end of the breeding season, when the harems are disintegrating and the harem bulls are returning to sea, the virgin females come ashore, and at least some of them are fertilised by the young males which have not maintained harems."

While at sea the females are solitary or only slightly gregarious. Even at the peak of the annual migration at sea one ordinarily sees only single individuals, or at most a group of half a dozen scattered over half a square mile. They leave the water one by one and establish themselves individually in the rookery. Their arrival is spread over a period of more than six weeks so that females in various phases of the reproductive cycle are present on the rookeries at all times during the breeding season. The arriving females are in the terminal stages of pregnancy. Although occasional cows bear their pups within an hour of arrival on land, the usual interval is about two days. It was found (Bartholomew & Hoel, 1953) that the female comes into œstrus about six days after parturition, returns to the sea one day after the onset of œstrus and spends most of the rest of the summer at sea. The duration of the first trip to sea averages 5 days, and the duration of second and subsequent trips to sea averages about 8 days. The females stay ashore two days or less between trips. Since the females nurse only their own young, the pups are usually unattended and go without eating for a week or more at a time. Thus, the contacts of the pups with their mothers constitute only a small part of their total social

contacts and occupy only a small part of their time.

Methods

The material presented in this study was obtained during the summer of 1951 when slightly over 220 hours were spent observing a group of 20 fur seal harems in Kitovi Amphitheatre, on St. Paul Island in the Pribilofs. During the breeding season approximately 1,600 individuals (including cows, bulls, and pups) occupied the study area. Tabular records were kept of all types of behaviour which were frequently repeated and detailed written descriptions were made of all activities which appeared to be significant. At the onset of the study as many animals as possible were marked either with flipper tags to which coloured strips of plastic were attached (Scheffer, 1950) or by splotches of quick-drying paint applied with a cloth dauber attached to the end of a heavy bamboo pole. Many adults could be recognised by scars, injured flippers or other individual characteristics. In one way or another it was possible to recognise all 20 of the harem bulls in the study area, 40 females, and 20 pups. In addition it was possible to keep track of many cow-pup pairs for a few hours and in some cases for as long as two days on the basis of location, and individual characteristics. Once the animals had been marked they were not molested in any way. All observations were made from a small blind on a cliff overlooking the amphitheater. The only disturbances were the arrivals and departures of the author and the animals soon became habituated to his activities to such an extent that no perceptible response greeted his appearance.

Births and Associated Activities

1. Parturition

Delivery is rapid, expeditious, without apparent preparatory behaviour, and without elaborate postnatal activities. Scores of births were observed, but it was never possible to tell precisely when a cow was about to deliver except by noticing the appearance of the whitish amniotic sac in the vulva. Prior to and during parturition the females held shoulders, fore-quarters, and flippers in the usual standing posture, rotated the pelvis through 90 degrees to either right or left and extended both hind flippers cephalad thus exposing the perineum and keeping it free of contact with the ground. This posture is often assumed at other times also.

The females rarely remained motionless in this posture for long, but moved about or shifted position. Their restless behaviour often disturbed adjacent females who threatened them or reacted aggressively and it frequently excited the nearest harem bull to vigorous efforts at harem maintenance, including energetic herding of the parturient female and other nearby cows. These activities in turn often aroused other adjacent bulls to energetic harem maintenance with the frequent result that the female delivering her young became the centre of a flurry of violent activity. As the parturient cow fought off the other cows and attempted to avoid the bulls, the half-born pup was often battered against the rocks and sand in a most severe fashion. In the few instances when a female happened to occupy a relatively secluded spot in the rookery, she was of course able to bear her young with a minimum of disturbance. Occasionally, the pup's advent into the world was unbelievably violent: the moving about of the cow sometimes was such a strong stimulus to the bull that he rushed over and picked her up in his teeth and tossed her back into his harem. In one instance a cow in labour was seized simultaneously by two bulls, lifted clear of the ground and used like the rope in a tug-of-war—all the while with the pup partly extruded. When undisturbed, the females usually assumed the "birth posture" first on one flank and then the other. During labour they almost invariably moved about and shifted position, bumping the head of the pup on the sand and rocks with every step. They give no oral assistance to the delivery of the pup, umbilical cord, or placenta.

The young are normally born head first, and in the 21 births observed in which the females perineal region was visible only 3 cases of posterior presentation were noted. The amnion normally remained intact until most of the head was extruded. In one instance delivery was completed with amion completely intact and it was ruptured only when it began to slide down the rocky slope onto which it had been delivered.

The duration of parturition, measured from the first appearance of the amnion in the vulva to the complete birth of the pup, is often very short. This interval was timed in six instances with the following results: 52 seconds, 2 minutes 30 seconds, 5 minutes 18 seconds, 7 minutes, 8 minutes, and 21 minutes. In the last case the female was being disturbed by efforts to mark her.

After delivery of the placenta the females

usually maintained themselves intermittently in the "birth posture" for several hours, although within seconds after birth they were able to move about agilely with no sign of disability.

It has been reported that female domestic mammals as diverse as sheep, dogs, and cats establish olfactory, gustatory, and tactile contact with the newborn by smelling and licking and that these stimuli facilitate the normal postnatal physiological adjustment of the young and also contribute to the appropriate orientation of mother to offspring. (See, for example, Collias, 1956: 229). Tactile contact with the newborn is minimal in the fur seal. Females were never seen licking or grooming pups of any age in any manner. Their primary sensory contacts with their young appeared to be olfactory and visual. During parturition the cow frequently turned and sniffed at the partly extruded fœtus. Quite often adjacent females observed the cow in labour with apparent interest and smelled the partly born pup, but showed no further response. The only gustatory contacts observed took place in the infrequent instances when pieces of the amnion adhered to the pup, particularly in the head region. In such cases, a few minutes after the completion of delivery the mother tugged haphazardly with her teeth at the remnants until they pulled free.

Although it is common for mammals to eat the foetal membranes and placenta, this has never been reported in the Alaska fur seal nor was it ever seen by the writer. Ordinarily the pup's struggles free it of the amnion without assistance from the mother, but the umbilical cord is remarkably tough and often remains intact for some time. Neither the pup nor the cow pay any attention to it. Indeed, the umbilical cord frequently remains unbroken for a day or more. In unusual circumstances a pup may laboriously drag its placenta about through the rookery for a week before the umbilical cord breaks. It is commonplace to see a pup struggling to pull free from a cow or a bull that is standing or lying on the pup's placenta. In rocky areas the placenta occasionally gets stuck in a crack or under a ledge and the pup may struggle intermittently for hours before it pulls free.

Since fur seals do not eat the fœtal membranes and thousands of births occur in the congested rookeries, the placentas represent a large source of pollution. The seals crawl over them and lie on them as if unaware of their existence. These afterbirths are an important food resource for the Arctic foxes (*Alopex lagopus*) which occur in large numbers in the Pribilofs. The foxes regularly patrol the inland fringes of the rookery and scavenge the placentas, frequently carrying them back to their burrows as food for their young. Glaucous-winged gulls (*Larus glaucescens*) also regularly eat the placentas. However, the supply far exceeds the demand and most of the placentas slowly disintegrate on the rookery during the breeding season.

2. Reaction of Female to Newborn

As described above the cow sniffs vigorously at her pup, apparently smelling it during and immediately after parturition, but does not groom or lick it. The cows show some solicitude for the newborn during the first few postnatal hours and they often lie in such a position that they shield their pups with their bodies from other animals. During the marking activities it was often found difficult to remove new-born young from the harems, not only because of the extreme aggressiveness of the bulls but because of the females' vigorous efforts to keep us from their pups. The observation area was a steep rocky slope worn smooth over the centuries by the movements of seals. Sometimes the new-born pup slid down a slope made slippery by rain, blood, amniotic fluid, urine, and fæces to lodge in a crevice several yards away, often in a different harem. The cow usually retrieved the pup by carrying it in her mouth for a few feet to some relatively undisturbed spot, or if the distance were more than a few yards, she simply moved into the new harem and joined her pup. These activities often involved a cow's shifting from one harem to another, consequently the retrieving of a pup was apt to be hampered by the harem bull in whose territory it had been born, because the bull tries to stop any female from leaving his territory regardless of her reproductive condition. The cows also bite and snap at any female that disturbs them, so that persistent but intermittent effort was usually required before a cow succeeded in retrieving or joining her pup. Retrieving of pups may take place either before or after delivery of the placenta.

Except in the hours immediately following parturition, the cows make no attempt to retrieve or carry their pups, but seek them out and lie down beside them where ever they may have wandered. Only once were two cows seen competing for the same pup. In this case a pup slid

down a slippery surface as soon as if was delivered and its fall broke the umbilical cord. Its mother, attempting to retrieve it a few seconds later, seized it by the skin on its back and started to lift. As she did so, a pregnant cow against which the pup had fallen seized one of its hind flippers in her mouth and a tug-of-war ensued. First one cow and then the other would lose her grip and then seize whatever part of the pup she could reach. The tussle went forward spasmodically for almost 40 minutes. The pup finally ended up a few feet away from the pregnant female, whereupon its mother lay down beside it and the incident was closed. Despite the rough treatment the pup did not appear to be seriously injured. One stillbirth was seen. The lifeless pup slid a few feet away from the mother who turned and retrieved it. After retrieval she paid no further attention to it and half an hour later she was lying on it asleep.

The females remain closely with their offspring for the several days between parturition and œstrus. During this interval, which averages six days in length (Bartholomew & Hoel, 1953), the female moves about very little, and usually remains close to the spot where she bore her pup: the pup spends much of its time nursing or sleeping. During this period the cows are relatively solicitous of their young, particularly during the first day when they can occasionally be seen carrying them out of the way of a rampaging bull or herding them away from a fight between bulls. When pups were being marked at the onset of the study it was found that the cows were extremely persistent and vigorous in their efforts to keep the observers from their pups—repeatedly attempting to bite, trying to walk off with their pups in their mouths, or seizing a pup on which they were working and trying to pull it away from them. This maternal solicitude, however, is brief and after the cows have been served and gone to sea they do not appear to defend their young in any manner, their only concern apparently being to suckle them.

The cows (and also the bulls, pups, and bachelors) pay no attention to the many dead pups that litter the rookery, walking or lying on them as if unaware of their existence.

Behaviour of Pups During and Immediately After Parturition

Typically, the pup remains completely flaccid during parturition, although one pup was seen to gape twice when only its head and shoulders were delivered and another breathed a few times while its hind quarters were still undelivered. When the head is presented the eyes and nostrils are closed, but by the time the shoulders are extruded the eyes are usually open. Usually 15 to 45 seconds elapse between completion of delivery and the time the pups stand up and vocalize, although sometimes the interval is as long as three minutes. The pups are capable of shaky but effective locomotion a few minutes after birth and appear to be as well co-ordinated then as they are several days later. Even while they are still attached by the umbilical cord to the undelivered placenta the pups perform many of the movements typical of the older pups and adults—shaking off water, snapping and biting at other animals, and scratching dog-fashion with one hind flipper. There seems no alternative to assuming that these complex and characteristic motor patterns are genetically controlled. The pups also frequently attempt to suck before the placenta is extruded—sometimes within less than five minutes *post partum*.

Changes in Pup Behaviour

The precocious nature of the pups and the lack of parental attention make it of particular interest to follow the changes in behaviour which accompany their physical maturation and to analyse the factors which allow them to fit into the social structure imposed on the breeding aggregation by the sexual and aggressive behaviour of the adults.

After a female has come into œstrus she spends not more than one day out of each week ashore. The bulls are completely indifferent to the pups at all times. As a result, aside from receiving nourishment from their mothers, the pups are completely independent of the adults during all but the first few days of their life in the rookery. Furthermore, since the cows rebuff all pups which are not their own and the bulls act as if the pups did not exist, the pups usually receive only violent (and sometimes damaging) incidental attention from the adults of their own species. During much of the breeding season the pups comprise by far the largest class in the fur seal rookery, because the cows spend most of their time at sea and the harem bulls prevent the non-territorial males from participating in the species' breeding activities. The pups form an essentially structureless social group; yet as a result of their gregariousness, their interactions with the bulls, cows, bachelors, and their responses to the terrain and to the ocean shore,

they have a characteristic distribution in the rookery.

1. Gregariousness

After their mothers have come into œstrus and departed for sea the pups are completely unattended. Like adult fur seals of both sexes the pups appear belligerent and aggressive; only a few minutes after birth they protest and snap at any creature which disturbs them. Despite this precocious belligerence their gregariousness is clearly apparent. They form compact aggregations (pup "pods") which are a prominent and persistent feature of the rookery. The pods form wherever the concentration of adults is minimal and disturbances are relatively infrequent. Consequently the pups accumulate like flotsam in the eddies and backwaters of the swarming rookery. Early in the breeding season while most of the pups are quite young the pup pods are small, but they increase with the growth of the population of pups. By the first week of July, pods of several dozen are commonplace; later in the season aggregations of several hundred individuals may develop. The very young pups have no apparent interest in the water. During the first weeks of life they tend to move inland and up hill so that the first pup pods form on the inland ledges of the rookery. This, of course, is most obvious in the steeper parts of the rookery. One frequently sees a pup struggling unsuccessfully for five or even ten minutes to ascend a slippery slope. Although they do not hesitate to go down gentle slopes very young pups rarely descend steep slopes, although they often fall off ledges or slide downhill. This tendency to move uphill has considerable survival value in that it takes the animals that were born in surf-washed areas up onto dry land and keeps pups away from the areas of maximal adult activity. As the pups mature this tendency to move uphill becomes less obvious and they wander widely about the rookery.

As the outlines of the harems change with the waxing and waning of the cow population, the shape and size of the pup pods alter. Early in the breeding season the pups do less wandering than later and the rookeries are also more crowded early than late. As a result the pup pods are most compact and sharply defined in the first third of the breeding season. At first the pups spend much of their time sleeping in the pods, but by early July they begin to tussle and play with each other very much like dog puppies. As the season advances this play-fighting becomes more vigorous and widespread and strongly suggests an infantile version of the contests between the bulls.

The behaviour of the pups in the pods follows an irregular but repetitious pattern of alternating quiet and activity. At one time 80 per cent. or more of the pups in a given pod will be asleep with the others tussling and playing or engaged in the incessant scratching so characteristic of the species while on land. Half an hour later almost all of the pups will be awake and active. These alternating periods of rest and activity follow no diel pattern which could be discerned.

2. Wandering

As the season advances the individual pups wander more and more widely over the rookery. By the time they are three to four weeks old they move about freely through the rookery, avoiding the bulls, dodging the cows, and generally exploring the terrain. In one instance a marked pup, 23 days old, wandered through 8 different harems in a 12-minute period. Similar performances were repeatedly observed with unmarked pups of unknown age. Sometimes several pups would wander about together in a loose group although in such instances they tended to stay in the more open and unoccupied parts of the rookery. The persistence of these exploratory activities was impressive. Pups would struggle through rough, almost impassable terrain, dodge adults, and would sometimes travel without stopping for as much as 200 feet from their point of departure. Despite this wandering, the pups spent most of the time in the general area where they were born (judging by the activities of the marked individuals). The wandering is so extensive that by the time the pups are a month old they appear to be thoroughly familiar with the terrain and the territorial boundaries within 75 yards of the area in which they were born.

3. Play

Like the young of many mammals fur seal pups spend considerable time in play. Much of this play, of course, is of a diffuse, erratic sort, but some of it foreshadows adult reproductive and aggressive behaviour and some of it contributes directly to mastery of the aquatic environment.

Copulatory play. During the first months of life the pups are continuously in the presence of overt reproductive activity, and this may have some bearing on the fact that they occasionally show in their play precocious copulatory be-

haviour. In five different instances prolonged and remarkably adult sessions of copulatory play were observed between pairs of pups that were one month or less *post partum*. In each case one pup was lying on its belly apparently asleep and another pup mounted it and performed an awkward but clearly recognisable series of copulatory movements complete with neck rubbing, grasping of the "female's" shoulders, and vigorous pelvic thrusts. The genitalia were never in more than approximate juxtaposition. Three of the performances continued for over one minute. In one case the "male" partner slipped off several times but remounted each time. In one case mounting was preceded by the vigorous sniffing by the "male" of the "female's" genitalia, behaviour which characteristically precedes the copulation of adult fur seals. In all cases the "female" participant was either completely passive or attempted to crawl away.

There are reports of bachelor fur seals maintaining "harems" of pups just as the bulls maintain harems of cows. Although nothing so highly organised was seen, a prolonged and vigorous copulation forced by a bachelor on a pup about three weeks old was in fact observed. My attention was attracted by what appeared to be a female treating a pup with unusual roughness even for a fur seal. The "female" proved to be a three or four year old male. Several times it picked the pup up in its mouth, shook it violently from side to side and dropped it. Then it threw itself onto the pup and began to make powerful pelvic movements. The bachelor pinned the pup down in the female copulatory posture and continued to make vigorous pelvic thrusts with penis extruded. Twice he succeeded in placing his penis between the anus and the scrotum of the pup. The movements could hardly have been more vigorous and determined and the pup struggled and bleated continuously. This activity continued for a little over three minutes until one of the adjacent harem bulls charged over to chase the bachelor. The bachelor released the pup, slipped into the water and swam away. The pup then joined one of the pup pods. Whether or not it was injured could not be determined.

It is of interest that adult female fur seals as they approach œstrus occasionally carry out elaborate homosexual pseudocopulatory manoeuvres. Usually one female assumes the male role and mounts another female which remains relatively passive while the active animal carries out the usual pelvic movements. Sometimes, however, the animal in the female role becomes active, assumes the usual female copulatory posture with flexed back and extended flippers; and the two animals then perform a remarkably realistic pseudocopulation. Harem bulls watch the performance without apparent reaction.

Swimming. Fur seal pups receive no parental instruction or help in swimming. During the first couple of weeks of life they show no overt interest in the water. They are, however, apparently able to swim almost from birth. At high tide during a storm an enormous wave washed from the rocks a pup which could not have been more than a day or two old. Despite the violent surf and the fact that it had never been in the water before, the pup swam well enough to keep head above water. Several times waves deposited it on the rocks and it managed to crawl clumsily upward for a few feet before again being swept out to sea. Two other similar instances were seen.

As described in a previous section, in the early part of the breeding season the pups tend to confine their activities to the inland parts of the rookery, but as the summer advances they wander widely and make frequent excursions to water's edge; this may involve wending circuitously through the territories of several bulls. At first the pups merely stand or wade about in water a few inches deep. In the area being studied this type of play began abruptly on July 20th. Five pups about three weeks old were seen wading in water 6 to 10 inches deep. Thereafter with each passing day more and more pups played in the shallow pools at the water's edge. They spent much time shaking, rubbing, scratching, and grooming, presumably in relation to the heavy infestations of ectoparasites which many of them carry. Frequently a pup stood in water 8 to 12 inches deep, thrust its head under water and looked about in an exploratory manner for 15 to 20 seconds. As the pups played in the shallow water they occasionally slipped off the rocks into water deep enough to force them to swim. They swam awkwardly but effectively with head and shoulders high out of water and front flippers performing a quick jerky "flying" motion. They appeared gradually to gain confidence and ventured farther and farther from shore, first swimming from rock to rock and later swimming a few yards out to sea. This aquatic behaviour appeared to be play and the pups chased and tussled in the water just as on shore. By the end of the fourth week in July the shoreline not exposed to heavy wave action was alive with pups crawling and squirming like

maggots. As the summer progressed they spent more and more time actually swimming. By the first of August pups frequently played and chased in the kelp 25 to 50 feet off shore. They still swam high in the water and when they dived they never appeared to go more than a few inches beneath the surface.

Recognition of Parent and Offspring

The data from marked cows and pups presented by Bartholomew & Hoel (1953) confirmed the long-standing assumption that the cow fur seal would nurse no pup but her own. Observations of the behaviour of these marked animals affords considerable insight into the mechanism by which mother and offspring locate each other in the confusion of the rookery.

When one considers that there are almost one and one-half million fur seals on St. Paul Island and that the pup population alone numbers about 600,000 (Kenyon, Scheffer & Chapman, 1954) it is apparent that the primary orientation of the mother fur seal to her offspring must be geographical. She cannot possibly find her pup unless she returns to the part of the island where she left it, and the pup cannot possibly be found unless it remains in the approximate area that it occupied during its parent's previous stay ashore. Thus, in the location of the pup by its mother, familiarity with topography and individual attachment to certain specific localities is of primary importance just as it is in most other aspects of the fur seal's activity ashore.

During this study there were scores of opportunities to observe the way in which lactating females returning from a week or more at sea found their own pups in the appalling confusion and congestion of the rookery. The process can be divided into three stages. The length of these stages and the details of the activity characterising each vary from instance to instance, but the general pattern is relatively constant. First, the female comes ashore in the immediate part of the rookery where she had born her pup. During the cow's absence the pup wanders considerably but spends most of its time near where it had been born. This geographic localisation ensures that the mother and her offspring will probably be in the same general part of the rookery when the female returns from her long stay at sea. Second, the female utters a characteristic prolonged vocalisation which is readily recognisable above the cacaphony of sound of the rookery as a whole. This call which sounds like the bawling of a calf is so distinctive that whenever a female in the study area emitted it she could be located within two or three seconds no matter where she was, and presumably the pups could do as well particularly because they had the motivation of hunger. Third, as soon as the wet and shiny females come ashore and gives this vocalisation, any hungry pups which may be in the vicinity immediately move directly and rapidly toward her with necks extended and muzzles pointing at her. Characteristically she sniffs vigorously at their noses. If the pup is not her own, she either ignores it thereafter or darts her head out in an open mouthed threat at the pup which then retreats hurriedly. If the pup is her own, she merely stands quietly while the pup moves to her side and muzzles about looking for a nipple. Although the number of tagged pups was too small to give adequate evidence on the point the impression was gained that the pups which had recently fed tended to stay in the pup pods while those pups whose mothers had been away at sea for several days were restless, wandered about, and spent considerable time greeting females as they came ashore. In two of the scores of cases observed the first pup which reached a cow when she hauled ashore and bawled was accepted by her. Usually, however, a period of erratic and rather leisurely search intervened in which the female moved slowly about the rookery, avoiding the bulls, bawling at intervals, and sniffing at the noses of pups which approached her. In one case a cow was seen to sniff 19 pups during 24 minutes without finding her own, and in another a female sniffed 14 pups in six minutes before finding her own.

Since many pups die some of the cows never find their pups. The writer had the good fortune to be able to make a series of observations on a marked female which failed to find her pup. She came ashore at 12.30 p.m., July 24th, wandered about erratically in the vicinity of the harem where she had been marked and examined many pups which came up to her, but accepted none. She slept most of the afternoon, but three times she roused and wandered about apparently looking for her pup. At 8.00 the next morning she still had not found her pup and occasionally moved about in her usual area. At 2.08 that afternoon she stood up, walked directly to the water and swam out to sea. Her stay at sea was very short for she was asleep in her usual area at 1.00 p.m. on July 26th, but still without a pup. For these observations and from the evidence adduced elsewhere (Bartholomew & Hoel, 1953), there seems to be little doubt that a female fur

seal will not suckle at all if her own pup is not available. This selective recognition appears to depend exclusively on the cow. Pups often attempted to suck cows that were not their mothers and in several instances pups were seen nuzzling about in the axillary region of sleeping bulls, apparently trying to suck.

Discussion

Because of the extreme reduction of parental care, the remarkably advanced state of development of the pup at birth, and the infrequency of feeding, knowledge of parental and ontogenic behaviour in the Alaska fur seal appreciably extends the spectrum for mammalian social behaviour. Nevertheless, it can readily be fitted into the picture obtained from other and dissimilar mammals.

Geographic Localisation

Except for some cetaceans, and possibly a few bats, no mammals travel more extensively than do Alaska fur seals; nevertheless, precise geographic localisation is the keystone of the behaviour of the principal classes of the breeding population—harem bulls, cows, and pups. The harem bulls are territorial in the strict sense of the term—defence of a specific area. The cows and pups have a definite home range on shore but show no territoriality. The home range of a cow need not correspond with the territory of any particular bull although a cow's sedentariness during the interval between parturition and œstrus usually results in her being served by the male in whose territory she bore her pup. The pups tend to stay in the same general area where they were born although their home ranges do not coincide with the territorial boundaries of the bulls and the home range of any given pup is probably more extensive than that of its mother. The pups tend to remain in areas outside the territories of the bulls because they actively avoid the males whose violent activities represent a major source of danger to them. Thus the organisation of the breeding population of fur seals has as its keystone topographic orientation, but the pattern of this orientation differs for each class of the population on the rookery. The bulls defend a territory; the cows during their brief stays ashore seek out the area where they bore their pups; and the pups wander extensively but centre their activities in the general area where they were born.

The pups' topographic orientation appears to be a direct outgrowth of investigative behaviour which by the time a pup is two or three weeks old has led to a detailed familiarity with the nearby rookery, not just its birth site.

Precociousness

Although many special attributes of the bull and cow fur seals are essential to the maintenance of the unusual pattern of the species' reproductive behaviour, the precociousness, vigour, and independence of the pups during their first weeks of life are capacities without which the existing patterns of adult reproductive behaviour would be ineffective.

Precocious young are characteristic of all members of the family Otariidæ, but detailed ontogenetic data are available only for the Alaska fur seal which is the most precocious species known in the order Carnivora. At birth Alaska fur seals are as advanced as domstic dogs about 3 weeks old. Scott & Marston (1950) have studied the "critical periods" in the ontogeny of domestic dogs and proposed four principal behavioural periods; *neonatal* (birth until eyes open), *transition* (from opening of eyes until leaving the nest), *socialisation* (leaving of nest until weaning), *juvenile* (weaning until sexual maturity). At birth the fur seal pup is in about the same stage of behavioural development (except for feeding) as the domestic dog at the end of the "transition" stage, and because of the crowded nature of the rookery, the "socialisation" period of the fur seal pup may be said to begin at the instant of birth.

Socialisation

The primary socialisation of fur seal pups is to other pups, rather than to the adults of either sex. The bulls are ordinarily completely indifferent to the pups; the pups actively, sometimes almost frantically, attempt to avoid the bulls whenever the latter are in motion, for the violent aggressive behaviour and harem maintenance of the bulls often hurts the pups and occasionally injures or kills them (Bartholomew, 1953: 495). The cows are either indifferent to or aggressive toward all pups but their own. Moreover, except for the first few days post partum the pups are only infrequently in contact with their mothers. Consequently, the pups are usually rebuffed in all their social contacts except with other pups. The social importance of pups to each other is further strengthened by their habit of spending most of the time together in the pup pods. A similar dependence of pups on each other for socialisation has been reported

in dogs and wolves (Scott, 1950) but in these canids the socialisation depends on litter mates rather than on unrelated members of the same age class. It is interesting that a social structure based in large measure on year class is maintained for the first several years of life by fur seals, particularly the males.

Social Dominance

Although aggressive behaviour could hardly be more conspicuous than among fur seals, dominance orders, although possibly present temporarily among adjacent females are not an obvious element within any age and sex class of the population. Clear-cut dominance relations exist between the various classes, of course.

Summary

Parental attention of Alaska fur seals is minimal. The bulls ignore the pups. The cows rebuff all pups but their own. Birth is rapid and delivery usually takes less than 10 minutes. The fœtal membranes are not eaten, nor is the umbilical cord bitten. The females smell but do not groom or lick their freshly delivered pups. In the first hours after giving birth, the female will retrieve her pup if it is displaced and also will carry it in her mouth away from danger or disturbance. She threatens and bites other females that disturb either her or her pup. This attentive and protective behaviour is confined exclusively to the few days between parturition and œstrus and is conspicuous only for a period of a few hours to a day post partum.

Pups can locomote and vocalise within a minute of birth. Nursing may begin within a few minutes of birth. Even before the umbilical cord is broken, they scratch, shake off water, threaten, and vocalise in the manner characteristic of their species.

A hungry pup will attempt to suck any female but a female will suckle no pup but her own. Since post œstrus females spend not more than one day per week ashore, the pups are unattended most of the time. When a female returns from the sea, local geography supplies the primary cue for finding her young. She comes ashore in the general area where she bore her pup (the pup remains in the same general vicinity) and gives a characteristic vocalisation. She is at once approached by the numerous hungry pups in the vicinity. She sniffs at each as it approaches and threatens all except her own, which she allows to suck. If her pup is not one of those that approaches her, she wanders through the rookery calling and sniffing pups until she finds it.

Pups aggregate in structureless social groups which form on the rookery in areas of minimal disturbance. By the age of three or four weeks, they wander extensively in the rookery. Most of their time is spent sleeping, grooming, or play-fighting. Copulatory play may occur in pups less than one month old. The pups can swim at birth but avoid the water for the first three or four weeks of life. They receive no parental instruction in swimming or in anything else.

Fur seal pups are as advanced at birth as dog puppies at three weeks of age. Socialisation begins immediately after birth and after the age of one week is almost exclusively dependent on other pups. After the age of one week except for being suckled on about one day per week, the pups receive nothing but rebuffs and injury from the adults. They find their social ties almost exclusively with members of their own age class. This age class dependence in social contacts persists for several years, particularly in the males.

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REFERENCES

Bartholomew, G. A. (1953). Behavioural factors affecting social structure in the Alaska fur seal. *Trans. 18th North Amer. Wildlife Conf.*, 481-502.

Bartholomew, G. A. & Hoel, P. G. (1953). Reproductive behaviour of the Alaska fur seal, *Callorhinus ursinus*. *J. Mammal.*, **34**, 417-436.

Collias, N. E. (1956). The analysis of socialization in sheep and goats. *Ecology*, **37**, 228-239.

Kenyon, K. W., Scheffer, V. B. & Chapman, D. G. 1954). A population study of the Alaska fur seal herd. *U.S. Fish and Wildlife Service, Spec. Sci. Rept. Wildlife*, **12**, 77 pp.

Scott, J. P. (1950). The social behaviour of dogs and wolves: an illustration of sociobiological systematics. *Ann. New York Acad. Sci.*, **51**, 1009-1021.

Scott, J. P. & Marston, Mary-Vesta (1950). Critical periods affecting the development of normal and mal-adjustive social behaviour of puppies. *J. genetic Psychol.*, **77**, 25-60.

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THE INCIDENCE OF THE FOLLOWING RESPONSE AND THE DURATION OF RESPONSIVENESS IN DOMESTIC FOWL

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Introduction

The following response of newly-hatched nidifugous birds has been used by many workers to study the process called "imprinting" by Lorenz (1937). A survey of this work and a discussion of the theoretical importance of the imprinting process has been given by Thorpe (1956). Fabricius (1951) made the first attempt to analyse systematically the release of the following response and the imprinting phenomena associated with it in various species of ducks. Further important work of a similar kind was that of Fabricius & Boyd (1954) and of Hinde, Thorpe & Vince (1956). These confirmed many of the earlier observations on the following response and established the simplicity and lack of specificity of the sign stimuli releasing the response, the increasing selectiveness of the response with experience of the releasing stimulus and the specificity of the sensitive period for this process of imprinting.

Recently the study of imprinting has been transferred from the field to the laboratory, first by Ramsay & Hess (1954) and subsequently by Hess (1957) and Jaynes (1956, 1957, 1958a and 1958b). These investigations have been concerned with the sign stimuli releasing the response, the amount and kind of experience required to produce a selective response and the critical or sensitive period in which the experience must occur. The present paper gives the results of a laboratory experiment designed to give information concerning the relations between the amount of experience, the incidence of the following response and the duration of this responsiveness in domestic fowl.

Material and Method

The chicks used were hatched in the laboratory from eggs of a pure bred Rhode Island Red flock. In all 500 chicks were tested; with 2-4 dozen hatching each week the work extended over six months. The following response of each chick was tested the day after the day of hatching, so that the chicks were mostly 18-30 hours post-hatch when tested. For the first 12 hours between the time of hatching and testing they were kept as a group in the drying-drawer of the incubator and for the rest of the time they were kept in a covered cage equipped with radiant heat bulbs. After the first test the chicks were kept in groups in similar covered cages until the time of the second test. Apart from the brief moments of handling and feeding the chicks saw nothing outside their cages and the test alley.

The following response was tested by exposing the chicks to a moving box in an enclosed alley. This alley or "run" was 10 ft. × 2 ft. 6 in. × 2 ft. high and was lit by 60-watt radiant heat bulbs shaded from above and arranged along the top and to one side of the run. The cardboard box (8 in. × 6 in. × 6 in. high) was covered with red paper and suspended 2-4 in. above the floor by two wires from an overhead cord. By means of a pulley arrangement this cord could be moved by a handwheel and so the box moved up and down the length of the run. (An attempt to mechanise this part of the apparatus was abandoned as the slight noise of the motor appeared to inhibit the chicks.) The length of the floor of the run was marked off into six-inch sections and these were numbered so that the distance moved by box or chick could be recorded in six-inch units. The whole run was covered with muslin and the tests were carried out in a darkened room so that the chicks did not see the experimenters.

The procedure for testing the following response was as follows. The chick was placed in the run on the same side of the box as were the lamps (in this way the shadows cast by the box were on the side away from the chick), and at a point 2 ft., i.e. 4 units, from one end of the run and facing the far end at a distance of 8 ft. or 16 units. The chick was thus free to run in either direction, i.e. towards or away from the box when the latter began to move. The trailing edge of the box was also at the 4-unit position. One minute was allowed for the chick to settle down, the box remaining static except for some swaying. Then the box was moved with a jerk away from the chick until the trailing edge had moved through 2 units. It was then allowed to rest until five seconds had passed from the time of movement, and was then moved back slowly through

2 units, or back to the chick if the chick had moved part of this distance. A responsive chick would move up to the box or even beyond it. In all cases the box was returned so that its trailing edge was immediately in front of the chick. This second or return phase of movement was timed to take five seconds.

The whole process of movement, which took 10 seconds, constituted a stimulus sequence, which we shall call one experience. Such an experience was immediately followed by another, and so on. In this way a chick could be given 6 experiences every minute. Any movements made toward the box during the 10 seconds of an experience were recorded as one response. In this way a chick could make either one response or no response and could score 0, 1, or 2 units of distance in making a response. If a chick moved through 12 units, i.e. to within 2 ft. of the far end of the run, the direction of movement of the box was reversed. A responsive chick could thus move several times up and down the length of the run. The total number of responses made by each chick and the total number of units through which it moved during the responses were recorded and form the data of this experiment.

In the course of the experiment each chick received 2 tests. In all cases the first test was made on the day after hatching, but there were 3 different amounts of experience in this first test. One group of chicks received 50 experiences, a second group received 10 experiences and a third group received none although chicks in this group spent one minute in the run beside the stationary box. The times for these test treatments were approximately 9 minutes 20 seconds, 2 minutes 40 seconds, and 1 minute respectively. When chicks were given 50 experiences, the numbers of responses made and units moved during the first 10 experiences were also recorded.

The second test was carried out from 1-6 days after the first test. This second test followed the same procedure as the first but consisted always of 10 experiences only. Thus, there were 3 experimental treatments of 50, 10 and 0 experiences in a first test and 6 treatments—1 to 6 day intervals—for the second test, resulting in a total of 18 experimental groups. Each group was made to contain 25 chicks giving a total of 450 chicks for the main experiment. As far as possible chicks were assigned to each first test treatment so that each hatch was evenly distributed among the 3 groups, but usually the whole of a hatch was assigned at random to one of the second-test groups. In this way the chicks from one hatch were divided into 3 groups corresponding with the 3 degrees of experience in the first test, but all 3 groups were given the second test after the same time interval.

Results

The results were considered in terms of the numbers of responses made and the distances run by the chicks. They are given here in terms of the numbers of responses since the distance scores gave the same results, confirming the observation that once a chick began to follow it would usually run right up to the box when making a response. Those birds which made one or more responses in the course of a test have been classified as "followers" and those which failed to make at least one response have been called "non-followers". Birds that responded on one half or more of all the possible occasions (10 or 50 movements of the box) have been called "good followers". The numbers for both "followers" and "good-followers" are presented so that the effect of different criteria of response on the pattern of the results may be seen.

(1) Incidence of the Following Response

The incidence of following when first confronted with a moving object at 24 hours post-hatch is shown by the numbers of birds which made at least one following movement in the course of the first test. These figures are given in ordinary type in Table I, where the 18 groups of 25 birds per group are listed. They show that groups which differed only in the time of the second test did not differ in incidence of following in the first test, i.e. they all contained similar proportions of responsive and non-responsive birds. Groups which differed in respect of the amount of experience received in the first test differed also in the numbers of birds showing a response. In the "10 experiences" groups 86 out of 150 birds (57 per cent.) followed. In the "50 experiences" groups 120 out of 150 birds (80 per cent.) followed, 76 of them (51 per cent.) doing so during the first 10 experiences. The proportions of birds that responded during the course of 10 experiences are not significantly different in the "10" and "50 experiences" groups, but they are both significantly smaller than the proportion that responded in the course of the full 50 experiences ($p<0{\cdot}01$ using the modified significance test of Brown (1956) for the difference between two observed propor-

Table I. The Incidence of the Following Response in the Domestic Fowl.

1st test group / 2nd test group	"10 experiences" (1 min. with stationary box followed by 10 movements of box)		"10 experiences" (1 min. with stationary box, followed by 10 movements and a further 40 movements of the box)		"50 experiences"	
1	13	*10*	15	*4*	20	*15*
2	16	*10*	13	*5*	20	*11*
3	13	*6*	14	*7*	20	*7*
4	12	*5*	11	*5*	18	*7*
5	19	*12*	16	*8*	22	*12*
6	13	*6*	7	*3*	20	*10*
Total	86	*49*	76	*32*	120	*62*
Average for 6 groups	14	*8*	13	*5*	20	*10*
% age chicks responding	57%	*33%*	51%	*21%*	80%	*40%*

Numbers of birds in each experimental group of 25 chicks which followed a moving box when tested one day after hatching. The numbers in ordinary type are those that made at least one response, while the numbers in italics are those that followed on 50 per cent. or more of the possible occasions.

tions). Thus 10 movements of the box were sufficient stimulation to produce following in 50—60 per cent. of these chicks and increasing this experience by 5 times raised the incidence of following to 80 per cent.

The figure in italics in Table I shows the numbers of birds which responded on 50 per cent. or more of the possible (10 or 50) occasions. These birds were "good followers" and the response incidences for this degree of responsiveness were 33 per cent. for the "10 experiences" groups, 21 per cent. for the first 10 experiences of the "50 experiences" groups and 40 per cent. for the full 50 experiences. The proportions of birds that were "good followers" in the first 10 experiences (21 per cent.) and in the whole 50 experiences (40 per cent.) of the "50 experiences" groups differ significantly at the 1 per cent. level (Brown test), showing that the extra experiences resulted in more birds making high scores. However, the proportion of "good followers" in the "10 experiences" groups (33 per cent.) does not differ significantly from that for the "50 experiences" groups (40 per cent.) but is significantly greater than that for the first 10 experiences of the latter groups (21 per cent.) the difference being significant at the 5 per cent. level (Brown test). This shows that the "10 experiences" groups contained more highly responsive birds than did the "50 experiences" groups.

It would seem, therefore, that the incidence of following in a given group of domestic chicks was proportional to the amount of experience of the moving object, and that individuals varied in their readiness to respond as a result of factors other than the amount of experience of the box. Thus, some birds responded with the minimum of experience, whereas others required increasing amounts of experience before beginning to follow.

(2) The Duration of Responsiveness

The duration of the responsiveness to a moving object is shown by the incidence of following 1-6 days after the first experience. The numbers of birds in each group of 25 which made at least one following movement in the course of the second test are shown in ordinary type in Table II. These results are expressed graphically in Fig. 1. It can be seen that the incidence of following declines with the passage of time regardless of the amount of experience of the moving box, but that the level of incidence is higher in those groups which previously received 10 or 50 experiences than in the groups which had had no such stimulation.

For each day of test the differences in numbers of chicks responding in each of the 3 groups were tested for significance. The χ^2-test, corrected for continuity, was used when the expected frequencies of response were 5 or more. Otherwise, the Fisher exact-probability test was used, c.f. Siegel (1956), Fisher (1950). The results for the "50 experiences" and "0 experiences" groups differed at the 5 per cent. level of significance on the first and third days after the first test. The results for the "10 experiences" groups differed from those of the "0 experiences" groups at the 1 per cent. level of significance on the second day following the first test. A sequence of significant differences such as this makes it extremely improbable that the differences in performance between the experienced and non-experienced groups were due to chance. There were no significant differences between the "50" and "10 experiences" groups results in the second test except for the 3-day interval when

Table II. The Duration of Responsiveness of Domestic Fowl to a Moving Object.

Treatment in 1st test	"0 experiences" (1 min. with stationary box)		"10 experiences" (1 min. with stationary box followed by 10 movements of box)		"50 experiences" (1 min. with stationary box followed by 50 movements of box)	
No. of days after first test: 1	3	*0*	7	*2*	11	*5*
2	5	*1*	14	*8*	10	*3*
3	2	*2*	4	*2*	10	*3*
4	1	*1*	3	*1*	6	*0*
5	1	*0*	6	*1*	4	*1*
6	0	*0*	0	*0*	1	*0*
Total	12	*4*	34	*14*	42	*12*
% age of chicks in the test	8%	*2·5%*	22·5%	*9·5%*	28%	*8%*

Numbers of birds in each experimental group of 25 chicks which responded to 10 movements of the box in the second tests. The numbers in ordinary type are those that made at least one response, while the numbers in italics are those that made 5 or more responses.

the use of a one-tailed test gives a significant difference at the 5 per cent. level. Thus, it is uncertain as to whether 50 experiences had more effect on subsequent responsiveness than did 10 experiences, although the greater stimulation certainly resulted in a higher incidence of following during the first test.

Also included in Table II in italics are the numbers of birds in each group which made 5 or more responses to the 10 movements made by the box. These are the "good followers" and the totals in the Table show that there were more "good followers" among birds that had previously seen the moving box than among those that had not (14 and 12 compared with 4), but that the numbers of "good followers" in the experienced groups appeared to be independent of the amount of their experience.

If the incidences on the first 3 days after the first test (Table II) are compared with those of the first test (Table I) it will be seen that there was a decrease in responsiveness in the "50" and "10 experiences" groups during this period. The "0 experiences" groups had significantly lower response incidences at this time than did

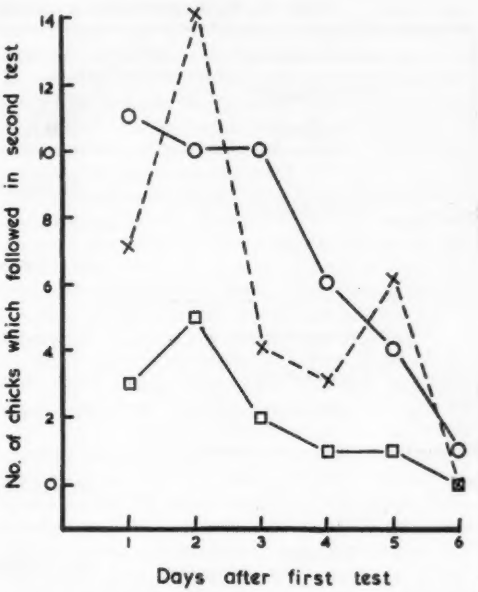

Fig. 1. Numbers of birds in each group of 25 chicks which made at least one response to 10 movements of the box in tests made from 1 to 6 days after the first experience.

— ○ — 50 experiences.
- - - X - - - 10 in the
— □ — 0 first test.

the "50" and "10 experiences" groups. There is no reason to suppose that the incidence of response in the "0 experiences" groups on the first day after hatching would not have been similar to those of the other groups in the first tests if they had received the same experience. There must have been, therefore, a much greater change in responsiveness in the "0 experiences" groups during the 2 days following the first test (2nd and 3rd days after hatching) than in the other groups and this difference can have been due only to the effects of the experiences of the first test. It is not clear from Fig. 1 whether this retarding effect on the loss of responsiveness in the "10" and "50 experiences" groups extends beyond the first 2 days after the first test.

(3) The Responsiveness of Individuals

So far the effect of the first treatment on subsequent responsiveness has been determined in terms of the proportions of birds in each group which followed in each test. It is instructive,

Table III. The Responsiveness of Individual Chicks of Domestic Fowl to a Moving Box

<table>
<tr><th>1st test treatment</th><th>1st test performance</th><th>2nd test performance</th></tr>
<tr><td rowspan="2">"0 experiences"
150 birds</td><td rowspan="2"></td><td>138 non-followers 92%</td></tr>
<tr><td>12 followers 8%</td></tr>
<tr><td rowspan="4">"10 experiences"
150 birds</td><td rowspan="2">64 non-followers 43%</td><td>55 non-followers 86%</td></tr>
<tr><td>9 followers 14%</td></tr>
<tr><td rowspan="2">86 followers 57%</td><td>61 non-followers 71%</td></tr>
<tr><td>25 followers 29%</td></tr>
<tr><td rowspan="4">1st 10 experiences
of
"50 experiences"
150 birds</td><td rowspan="2">74 non-followers 49%</td><td>62 non-followers 84%</td></tr>
<tr><td>12 followers 16%</td></tr>
<tr><td rowspan="2">76 followers 51%</td><td>46 non-followers 61%</td></tr>
<tr><td>30 followers 39%</td></tr>
<tr><td rowspan="4">"50 experiences"
150 birds</td><td rowspan="2">30 non-followers 20%</td><td>25 non-followers 83%</td></tr>
<tr><td>5 followers 17%</td></tr>
<tr><td rowspan="2">120 followers 80%</td><td>83 non-followers 92%</td></tr>
<tr><td>37 followers 8%</td></tr>
</table>

The chicks have been classified as "followers" and "non-followers" in each test according to whether they made at least one response or whether they failed to respond. The numbers of chicks in each category are entered in the table and the proportions in each sub-category are expressed as percentages.

therefore, to analyse the effect by considering the behaviour of each bird in the two tests. This is shown in Table III where the chicks have been classified in each test as "non-followers" and "followers" according to whether they made no response or whether they responded on one or more of the possible occasions.

The numbers in Table III may be conveniently compared with one another in terms of the proportions of "followers" and "non-followers" of the first test that followed in the second test. These proportions are indicated as percentages in the Table. Thus, in the "0", "10" and "50 experiences" groups 8 per cent., 14 per cent. and 17 per cent. of the first test "non-followers" followed in the second tests. This suggests that the experience of seeing the moving box without making any response had nevertheless had some effect on the subsequent responsiveness of the birds when compared with birds that had not seen the box move ("0 experiences" groups).

In the "10" and "50 experiences" groups 29 per cent. and 31 per cent. respectively of the first test "followers" responded during the second tests. This suggests that the extra 40 experiences of the "50 experiences" groups had not affected the subsequent responsiveness of "followers". However, the comparable value for those birds that began to follow in the first 10 experiences of the "50 experiences" groups is 39 per cent. and this suggests that the extra 40 experiences had increased the tendency of these particular birds to respond at a later date. Although the extra 40 experiences had induced an extra 44 birds to respond in the first test (Table III) only 7 of them responded in the second test, and this proportion (16 per cent.) is no greater than that for the "non-followers". This could mean that the act of following in these particular birds had not influenced subsequent responsiveness and that, therefore, it was the experience of seeing the box move which influenced subsequent responsiveness. If this were so, the "50 experiences" groups should have produced more followers in the second test than the "10 experiences" groups. It is possible that since the second tests consisted of only 10 experiences they were selecting for "quick responders". If "quick responders" tended to remain "quick" and "slow responders" tended

to remain "slow" in responding then the same second test results would be expected for the "10" and "50 experiences" groups since they had similar percentages of "quick responders" in the first tests; 57 per cent. and 51 per cent. respectively responded in the first 10 experiences.

In any case the second test results in Table III represent the combined results for different time intervals between the two tests and the results are too few and varied to permit any definite conclusions to be made as to the separate effects of seeing and following on retention of responsiveness.

Discussion

The results have shown that for a given hatch the proportion of birds showing the following response one day after hatching was dependent upon the amount of experience of the moving object. Furthermore, there were considerable individual differences in responsiveness in that different individuals required different amounts of experience before responding. Presumably, if given sufficient stimulation all the chicks would have responded. This agrees with the results of Jaynes (1958) who found that, at one day of age, 6 chicks given 40 minutes of experience of a moving box all responded by following. In an earlier paper Jaynes (1957) published a curve for the incidence of following after 30 minutes experience in groups of 5-7 chicks at different ages. The proportion of each group that followed varied from approximately 80 per cent. to 10 per cent. with age of exposure 1 to 60 hours. At 12-36 hours (the age at which our chicks were first tested) Jaynes obtained an incidence of following of approximately 50 per cent. This compared with an incidence of 51-57 per cent. and 80 per cent. for our chicks which received 1 minute 40 seconds and 8 minutes 20 seconds experience respectively, compared with 30 minutes experience of Jaynes' birds. These figures cannot be properly compared because the criteria of the response in the two experiments were very different. Thus, the incidences of following on 50 per cent. or more of the possible occasions were 21-33 per cent. and 40 per cent. for the "10" and "50 experiences" groups in the present experiment.

Although we have no data for differences in age earlier than one day, our results for a first experience on days after the first ("0 experiences" groups in Table II) show that there was a dramatic decrease in responsiveness during the second day. Some birds remained responsive although the proportion that did so was a variable and decreasing one and became negligible after 5 days. This picture is very similar to that given by Jaynes (1957b, Fig. 1) but is based on approximately five times as many chicks for each estimate and shows that for some birds the critical period was considerably extended. This latter circumstance has been reported for other species and treatments by Hinde, Thorpe & Vince (1956) and Fabricius & Boyd (1954). It might be thought that the "0 experiences" chicks in our experiment had become imprinted to the box which swayed slightly during their one minute in the run. In order to test this, 25 chicks were given 5 minutes each in the empty runway and were tested 2 days later with 10 movements of the box. Four chicks responded and this is of the same order of responsiveness as for the "0 experiences" groups. Another 25 chicks were given 5 minutes each in the run beside the stationary box. After 2 days interval 2 chicks responded to 10 movements of the box. This result agrees with that of the previous test, and this supports the view that the presence of the stationary box makes no difference to subsequent behaviour of the chicks. There is no doubt then that the critical period can extend beyond 3 days in individual cases.

The effect of the experience of a moving object at one day of age on the subsequent responsiveness of chicks in this experiment was not very great but from the amount of experience involved in the first test it is clear that the "imprinting process" is very "sensitive". As little experience as 10 short movements in 1 minute 40 seconds resulted in a detectable retention of responsiveness to the object. Five times as much experience, i.e. 50 movements of the box, also resulted in retention of responsiveness but the effect was very little more, if any, than that produced by the shorter period of experience. This is a surprising result in view of the fact that this extra experience induced more birds to respond in the course of the first test. It may be that the difference between 1 minute 40 seconds and 8 minutes 20 seconds experience was not enough to produce a significant difference in retention of responsiveness for there is evidence that a larger amount of experience does result in higher responsiveness at a later age. Thus in Jaynes' (1957) experiment, 30 minutes' experience resulted in a high proportion of his birds responding 10 days later. This is also borne out by later work by Jaynes (1958a). Hess (1957) has given evidence that in Mallards the degree of im-

printing is related to the amount of effort made in following rather than to the amount of experience. We were unable to find any relation between the distances run on first and second tests in our chicks, many very good runners of the first test failing to run at all during the second test and some poor runners of the first test following well in the second test. The individual records in Table III have suggested that "followers" in the first test were more likely to follow in the second tests than were "non followers" but that those that began to follow after 10 experiences were no more likely to respond on subsequent tests than were birds that had never followed. Since the second tests consisted of only 10 experiences it may be that they selected the "quick responders" and that the "slow responders" might have performed better than the "non-followers" if the second tests had been longer. Hence we were unable to decide whether or not the act of following affected subsequent responsiveness. The results do imply, however, that the act of following did not seem to affect the readiness to respond subsequently in that it did not tend to make "slow responders" become "quick responders."

There were some birds which did not respond in the first test but did respond during the second test. It is tempting to regard the behaviour of such birds as further evidence for Jaynes' "latent imprinting". This is the term he has coined for the phenomenon in which the groups of birds which he exposed to a moving box for 30 minutes at 2-4 days of age showed an increase in the proportion of followers when tested at 8 days of age, i.e. birds responded on test although they had not done so during the training session. In our experiment we had no such increase in proportion of followers, in fact the contrary was the case. The few birds which responded during the second tests but not to 10 or 50 experiences in the first tests were very slightly proportionally greater than those of the "0 experiences" groups which ran on test. It may be that seeing the box move did affect subsequent responsiveness in these birds but the differences in the numbers are too slight to decide. Since non-experienced birds may respond to the moving box up to five days after hatching it would seem that the responsiveness of an individual varies with factors other than age and previous experience. Further experiments on these problems are in process.

Summary

(1) Responses made by 450 day-old chicks either to a stationary box, or to one that made 10 or 50 movements, were observed. Their responses to 10 movements of the box were observed again on one or other of the 6 days following the first test.

(2) At one day of age over 50 per cent. responded to 10 movements and 80 per cent. to 50 movements of the box. Thus the incidence of the following response depended on the amount of experience of the releasing stimulus, but there was some variation between batches of chicks.

(3) The proportion of birds in each group which responded during the second test was inversely related to the number of days between the two tests, showing that responsiveness declined after the first day.

(4) A few birds responded on first seeing a moving box several days after hatching but none responded after five days. Thus the "sensitive period" for the following response may, in individual cases, be as long as one week.

(5) Chicks which had experienced a moving box at one day gave significantly higher response incidences at later days than those which had not seen a box moving before, though this difference tended to disappear by the fourth day. This suggests that some retention of responsiveness had occurred in spite of the very small amount of experience.

(6) There were no significant differences in responsiveness on later days between chicks which had previously seen 10 and 50 movements, though some differences were suggested especially between those that had responded in the first 10 experiences. Thus it is not clear whether the amount of experience determined the degree of retention of responsiveness.

(7) Birds that responded in the second tests tended to be those that had responded quickly in the first test but this may have been because of the brief nature of the second tests. There is, therefore, no evidence of the effect on subsequent responsiveness of the act of following.

(8) There was some indication that birds were more likely to respond for the first time during the second tests if they had previously seen the moving box one day after hatching, implying that seeing the moving box without responding may also have affected subsequent responsiveness.

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REFERENCES

Brown, J. (1956). A modified significance test for the difference between two observed proportions. *Occup. Psychol.*, **30**, 169-174.

Fabricius, E. (1951). Zur Ethologie junger Anatiden. *Acta Zool. Fenn.*, **68**, 1-175.

Fabricius, E. & Boyd, H. (1954). Experiments on the following reaction of ducklings. *Wildfowl Trust Annual Report*, 1952-3, 84-88.

Fisher, R. A. (1950). *Statistical methods for research workers*. Edinburgh: Oliver & Boyd.

Hess, E. H. (1957). Effects of meprobamate on imprinting in waterfowl. *Ann. N.Y. Acad. Sci.*, **67**, 724-732.

Hinde, R. A., Thorpe, W. H. & Vince, M. A. (1956). The following response of young coots and moorhens. *Behaviour*, **9**, 214-242.

Jaynes, J. (1956). Imprinting: the interaction of learned and innate behaviour: I. Development and generalization. *J. comp. physiol. Psychol.*, **49**, 201-206.

Jaynes, J. (1957). Imprinting: the interaction of learned and innate behaviour: II. The critical period. *J. comp. physiol. Psychol.*, **50**, 6-10.

Jaynes, J. (1958a). Imprinting: the interaction of learned and innate behaviour: III. Practice effects on performance, retention and fear. *J. comp. physiol. Psychol.*, **51**, 234-237.

Jaynes, J. (1958b). Imprinting: the interaction of learned and innate behaviour: IV. Generalisation and emergent discrimination. *J. comp. physiol. Psychol.*, **51**, 238-242.

Lorenz, K. Z. (1937). The companion in the bird's world. *Auk.*, **54**, 245-273.

Ramsay, A. O. & Hess, E. H. (1954). A laboratory approach to the study of imprinting. *Wilson Bull.*, **66**, 196-206.

Siegel, S. (1956). *Nonparametric statistics for the behavioural sciences*. New York: McGraw-Hill.

Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen.

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A CORRELATION BETWEEN POSTURE STANCE AND OUTCOME IN PAIRED CONTESTS OF DOMESTIC HENS*

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Staged pair contests between hens provide a simple and accurate test of the relative aggressiveness of two unacquainted individual hens. Extended series of such contests have been held in connection with attempts to find some of the factors that underlie the social hierarchy in flocks of domestic hens, (Allee & Foreman, 1955). It early became evident that some correlation existed between the postures of the two hens and the outcome of the paired contest. At first it was thought that the height of the head was important; later head position was observed to vary inconsistently, but at the same time closer observations revealed six distinct total body stances.

The most consistent and indeed the first observed consistent element in these stances was the degree of straightness of the legs, but other elements were found later which were also consistent. Three of the stances were named in prize fighting terms designating the relative degree of bending of the legs and body, i.e. semi-crouch, crouch, and deep crouch, with crouch being the medium or common posture. Because posture changes involve changes in the flexibility of the legs, the observer is advised to make all observations at "hen level" or very close to it, or the changes will not be seen.

Description of the Postures Observed

1. *Tall* (Fig. 1). The legs are quite straight and somewhat stiff. The breast is carried high; the tail is not spread; the wings are held high and tightly folded; the neck is often stretched, but may not be overly so, and the feathers are not fluffed. The posture is common in paired contests; in well organised flocks it is seen only when the flock is disturbed or when birds are unassimilated in the flock organisation. A bird may take this stance and give no other overt action to introduced birds either in the home flock or paired contest pen.

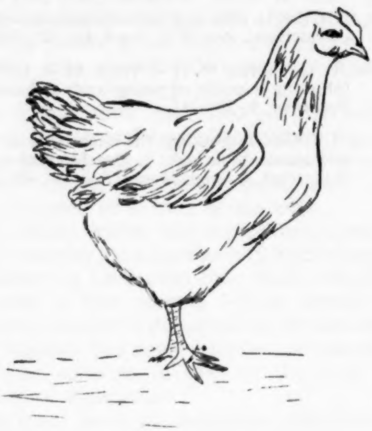

Fig. 1. Line drawing of "tall" to show the characteristics of this posture. Note the stiff legs, high breast and head, high tail and lack of wide tail spread. The feathers are not fluffed.

2. *Semi-crouch* (Fig. 2). The legs are flexed to some degree; the breast is high; the tail is spread; both wings are dropped, often far enough to make a straight line with the legs; the neck is usually less stretched than "tall" but may differ little in this one respect and the feathers are always fluffed. In paired contests the posture occurs in both normal and in hens injected with testosterone propionate (TP.). It is not seen in well organised flocks of hens except in hens injected with the androgenic hormone, testosterone propionate. This posture is the normal posture of dominant cocks, but is apparently more closely associated with dominance than maleness *per se* even among such cocks. Either cocky or henny waltzes may start from this posture. Cocky waltzing involves a strong back kick; primary feathers of the wing on the side opposite the object hen are spread and this wing is held forward. Considerable circular momentum is built up as the bird circles. Normal hens

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‡Deceased, March, 1955. This is part of a large body of research initiated by Dr. Allee. This paper was presented at the meetings of the Ecological Society of America at the University of Florida, 1954.

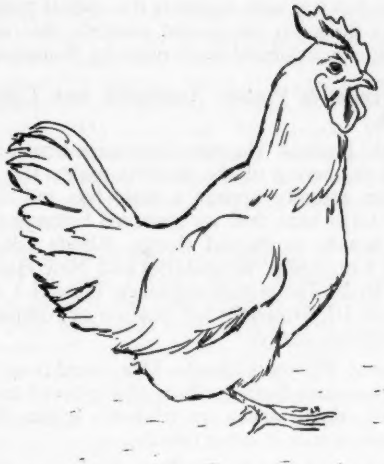

Fig. 2. Line drawing to illustrate the characteristics of "semi-crouch". The legs are bent, the breast and head are held high, the wings are down and the tail is very widely spread. The feathers are fluffed.

may occasionally approximate this behaviour pattern closely enough (but less emphatically) to lie within the normal variation of the male pattern. The henny waltz is much less emphatic; it involves a slow wheeling about the object of the waltz with some body tilt, no back kick and with wing primaries unspread. Normal cocks never do this henny waltz.

3. *Crouch* (Fig. 3). The legs are flexed and relaxed; the breast is in a normal medium-low carriage; the wings are not tightly folded but one may be dropped lower in a contest; if so the posture is called *3b*. The neck is usually not stretched, the tail spread is variable, but never as collapsed as in "tall' or "low". The feathers are fluffed out without being as much so as "semi-crouch" and "deep crouch." In some contests this posture appeared transitory between "semi-crouch" and "deep crouch". When the wing is not dropped this is the normal flock posture in a well organised flock. Indeed, the geometrical peck order with its complicated pecking relations shows no other type. The "crouch" is the normal posture among acquainted birds; newly-added birds can be readily distinguished in a well organised flock. The added bird will retain a posture (usually "tall") peculiar to its status until it is assimilated and becomes "crouched."

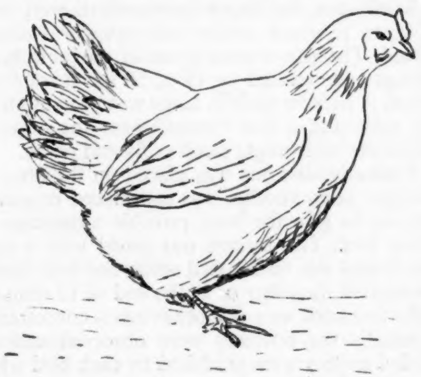

Fig. 3. Line drawing of "crouch" to show the characteristics of this posture. The legs are bent, the breast and head are held at medium height, the wings are held somewhat down, the tail is spread. The feathers are fluffed.

4. *Deep Crouch* (Fig. 4 & Plate IA). The legs are very bent, often one more than the other. The breast is held near the ground with one wing so close to the ground that it barely clears; the other wing may resemble the position in "crouch" but is usually lower. The neck is always drawn in close to the body; the feathers always fluffed, more so than in any other posture. "Deep crouch" is never seen in well assimilated flocks, but often is shown by the most aggressive hens in pair contests, and by aggressive birds away from their home flocks. Both cocky and henny waltzes may originate from this stance.

Fig. 4. Line drawing to illustrate the characteristics of "deep crouch". The legs are very bent, the breast and head are held close to the ground, the wings are held very low and the tail is widely spread. The feathers are very fluffed.

5. *Low* (Fig. 5 & Plate IB). The legs are very bent; the breast is almost parallel to the ground;

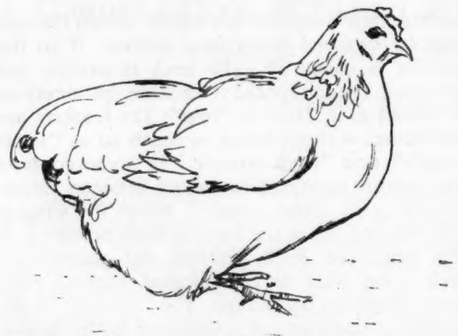

Fig. 5. Line drawing at "low" to show the posture characteristics. The legs are very bent, the breast and head are low but the head may be a little higher. The wings are held high and the tail is not spread. The feathers are not fluffed.

the wings are high; the feathers are not fluffed, and the tail is not spread; the neck may be somewhat stretched but is most often drawn in close to the body and low to the ground. "Low" is seen regularly in the peck order and when one bird tries to avoid another either before or after being pecked. The incidence of the stance is greater in the more typical of the straight line hierarchies than in geometrical ones.

6. *Sex Crouch* (Fig. 6). The bird's breast and tail, too, rest on the ground; the neck and head are held parallel to the ground; the wings are high and slightly spread at right angles to the body which favours mounting by the cock; and the feathers are not fluffed. Hens, even testosterone propionate-injected birds, seldom mount when presented with this posture. The "sex-crouch" may occur rarely in straight-line peck order if one of the high ranking members is a

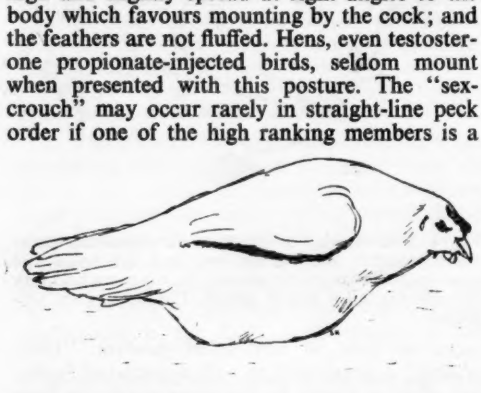

Fig. 6. Line drawing to illustrate "sex crouch". The head is extended forward parallel to the floor while the tail, unspread, extends posteriorly close to the floor. The weight of the bird is on its very bent legs which bring its breast and abdomen to floor level. The feathers are not fluffed.

tyrant, but it is seen regularly if a cock is present in any flock. In the paired contests that were tried it was exhibited most often by Bantams.

Differences in Posture Associated with Certain Breeds

Light Brahma. The extremely large breast and heavy feathering of the Brahma makes the tall posture actually appear a little less tall than other large hens that we observed belonging to such breeds as Barred Rocks, Rhode Islands Reds, Columbian Wyandottes and New Hampshire Reds. The picture sequence, Plate II A & B & Plate III, illustrates tall posture as compared to Leghorn stances.

Barred Plymouth Rock. This breed has the highest crouch from the floor of any breed tested and all other stances are relatively higher than the same stance in other breeds.

Anconas and Leghorns. These birds have long tails which are always spread in "semi-crouch", "crouch" and "deep crouch" postures. They also seem to fluff their feathers less in these postures, but this may merely mean that birds with thicker feathering more readily appear to be fluffed than those breeds with less plumage. Posture differences may occur in different strains of the same breed. For example, the Eberhard Leghorn stands in a high crouch with its long legs straighter and breast high, similar to the Ancona, whereas the Livengood Leghorn stands quite low in a crouch, resembling more the American breeds.

Results of Contests in Relation to Posture

Briefly put, the staged pair contests were held in a pen to which neither individual was accustomed. The pen was stripped of movable furnishings and reduced to 45 or 50 sq. ft. of floor space. A narrow built-in ledge was present along the sides and a low "stand" near the door to which the birds might jump or fly and perch.

Typically, one hen was placed on the floor of the pen; soon another was introduced in such a way as to give the least possible advantage to either bird. The contest was timed with a stop watch and was terminated when one hen clearly dominated the other or at the end of 12 minutes if the two hens were not behaving as contestants. Normally the postures were observed and recorded as they were exhibited by each bird while they were in the contest pen.

Three different series, each conducted in connection with the analysis of a specific problem and divided into two parts separated by 2-4

months, yielded useful data for the present study. Series I, staged to test the performance of dominant birds within each breed against each other, comprised 104 contests. Series II, staged to study the effects of testosterone propionate (Allee & Foreman, 1955) comprised 789 contests. Series III, staged to study the effects of increased light on aggressiveness, comprised 2,156 contests. Thus, the total number of contests yielding data was 3,049.

The data collected are summarised in Tables I to V. In the basic Tables I and II wins and losses do not balance, because postures were not recorded for both birds in all contests and because they were not recorded for either bird in some. Postures which were primarily concerned with balance (i.e. perching on the ledge) were not considered as these were not oriented to the contest in progress.

Results of the Contests in Terms of Posture Stance

To avoid complications, the terminal posture was used for all computations except in the table of initial postures and fights; in the latter the posture from which the fight began was listed. The tabulated data show that "tall", "semi-crouch", "crouch", and "deep crouch" are the most common postures and "crouch low wing" and "sex-crouch" are very much less frequently seen (Tables I and II). In addition, inspection

Table I. Postures of Individual Hens in Relation to Outcome of Staged Pair Contests, (Series I, II, and III).

Posture	Won	Lost	No contest	Fights
1. Tall	22	2204	248	0
2. Semi-crouch	821	2	63	180
3a. Crouch	966	4	152	131
3b. Crouch, low wing	62	0	11	*
4. Deep crouch	609	0	40	111
5. Low	0	108	28	0
6. Sex crouch	0	64	11	0
Sit	11	14	98	0
Total	2491	2396	651	422

*not separated from crouch.

shows that "tall" is a losing posture. It was associated with more "no contests" than any other and rarely preceded a win.

"Semi-crouch", "crouch", and "deep crouch" are the winning postures. All fights were preceded by one of these stances (Tables III and V): and "waltzes," when they took place, were given from "semi-crouch" and "deep crouch."

Postures "low" and "sex-crouch", frequently seen in heterosexual flocks, are associated with losing. They occur much less frequently than "tall." The "sex-crouch" was given mostly by Bantams in these contests but was also seen among other breeds when in the presence of an individual that was being injected with testosterone propionate (Series II, Table II).

The relationships between the terminal posture and the initial posture is seen in Table II. It is evident that there is not a great difference in these postures even though all stances of all birds were not catalogued completely. Many posture changes finally show a return to the initial posture, but some do not. The terminal postures, therefore, are slightly more accurate in terms of wins and losses than the initial ones. These data indicate that most contests are determined soon after the birds are placed in the contest pen. This same point is further shown by Table III, which shows that most posture changes occur without overt action on the part of the opponent. In fact more than four times as many changes occurred without a threat, peck or any other action by the opposing hen as occurred because of such actions.

In tabulations of posture data it should be remembered that for each pair contest there are two birds and therefore a minimum of two postures per contest. If changes in posture occur, of course, the number of postures per contest is correspondingly greater.

Fights are found twice in the tables. First they are listed in accordance with the posture held at the start of the fight, because the outcome may be influenced by considerations other than the aggressiveness of the opponents. Such factors as weight and fighting techniques are important in determining the winner of the fight. Taken alone, these factors may be quite unimportant in paired contests not ending in fights. Secondly, fights are listed in the series according to the total number of fights fought and breed involved, regardless of whether or not the posture was recorded (Table VI).

Additional tables (Tables IV and V) are included to show the results of contests in which

Table II. Posture of Individual Hens and Contest Outcome in Series II.

Posture	Won	Per cent.	Lost	Per cent.
Initial posture				
1. Tall	46	7·5	356	67·0
2. Semi-crouch	128	21·0	51	10·0
3. Crouch	235	39·0	55	10·0
4. Deep crouch	200	33·0	47	9·0
5. Low	1	·00	26	4·0
Total	611	99·5	535	100·0
Unaccounted for	178	23	234	30
Terminal posture				
1. Tall	21	3·5	384	71·1
2. Semi-crouch	117	19·2	30	5·5
3. Crouch	238	39·2	57	10·6
4. Deep crouch	229	38·0	43	8·0
5. Low	0	0·0	26	4·8
Total	605	99·9	540	100·0
Unaccounted for	184	23	249	32

Table III. Total Posture Changes of Individual Hens.

Series	No. breeds	Posture changes with threat	Posture changes without threat
I	7	11	24
II	6	24	242
III	7	181	676
Totals		216	942

both birds had the same postures at the time of the action of the contest. Only two results seem possible when both birds have "winning" postures (Table V), either they must fight or they must give a no contest. Since only two alternatives occur, one might consider the no contest seen here as a draw occurring because neither bird seems to want to press its aggression.

In the tabulation of these data one cannot overlook the rate of occurrence of "waltzes." It is apparent from Table VI that contests in which one or both birds were New Hampshires or Rhode Islands produced more "waltzes" than did all other breeds combined, although each breed had approximately the same number of birds under observation. This may be related both to their somewhat cocky fighting methods and to the greater incidence of fighting. Such behaviour did not, however, mean an invariable win by these breeds, as Barred Plymouth Rocks which showed a much lower incidence of this behaviour won more contests than any other breed. New Hampshires and Rhode Islands had a similar win record and were second to the Rocks in the total number of wins in paired contests. As can be seen from this table, there were six or seven breeds which could fight, but the great number of RI-NH fights indicates in addition to the above, that these breeds tended to fight each other more readily than they tended to fight other breeds or than other breeds tended to fight each other.

PLATE I

A. NH 49 gives a "deep crouch" to RIR 43. The "tall" RIR avoids. In all photographs the hens were apparently not disturbed by the photographic procedures. The fact that the RIR appears to be about to peck the NH is a common interpretation of some observers seeing this behaviour in newly organised flocks or paired contests. Pecking does not occur because the head is higher, since a peck may come from several head positions. Some tall birds look as if they could peck their opponents.

B. A "crouched" Barred Plymouth Rock is avoided by a "low" Ancona.

PLATE II

The following three illustrations are a photographic sequence showing a paired contest between Livengood Leghorn 68 and Light Brahma 5.

A. The Brahma is added to the neutral pen where the Leghorn sits. Note that the Brahma already shows the "tall" posture.

B. The Brahma walks to the rear of the pen as the Leghorn stands. This photograph shows very well the postures "crouch" and "tall" and the difference in leg flexibility.

PLATE III

The Leghorn threatens in a "deep crouch" and the Brahma avoids in a "low" posture.

Table IV. Results of Contests in which Both Birds had the Same Posture.

Series	Contest result	1. Tall	2. Semi-crouch	3. Crouch	4. Deep crouch	5. Low	Total
I	No contest	2	1	1	0	0	4
	Fight	0	4	2	1	0	7
II	No contest	10	2	4	0	0	16
	Fight	0	4	11	17	0	32
III	No contest	62	8	34	0	4	118
	Fight	0	45	28	8	0	81

Table V. Results from Combinations of Aggressive Postures.

Series	Contest result	2-4 Semi-vs. Deep crouch	2-3 Semi-vs. crouch	3-4 Crouch vs. deep crouch
I	No contest	0	0	0
	Fight	1	5	1
II	No contest	1	2	0
	Fight	11	9	7
III	No contest	5	24	5
	Fight	30	18	9

Table VI. Tendency of R.I.R. and N.H. to Fight*

Series	Total fights	Total no. breeds	No. of N.H. or R.I.R. involved in fights	No. of birds of all other breeds involved in fights	Waltzes N.H. vs. R.I.R.	Others
I	16	7	17	15	1	0
II	62	6	58	66	18	19
III	140	7	133	147	13	9
Totals	218		208	228	32	28

*Number of birds here is double the number of fights.

Other Behavioural Elements Associated with Posture

Hens in the contest situation may pick up shavings and drop them in a slow, emphatic fashion, particularly from a "deep crouch", or more rarely from a "semi-crouch". Those in a crouch may be seen quartering the floor as though looking for food. No eating occurs in the contest situation if food is kept out, and occurs rarely even if scattered grain or a concentrated food supply is present. Pecking shavings may be initiated by one bird in a "crouch" and taken up by the other with no relation to the contest in progress.

Flapping is of two types, one associated with the "semi-crouch" position and the other with "tall", "crouch", and "low". Flapping by a bird in "semi-crouch" is similar to the flapping of a cock before or after crowing. It does not involve posture change and appears to be aggressive. The second type is often, though by no means always, associated with posture change. It is a somewhat restricted flap with seemingly a less free swing of the wings.

Preening is not associated with change in posture and may occur from any stance except the "sex-crouch". If one hen begins to preen, the other often does likewise. Similarly clucking may occur from any stance, again except the "sex-crouch", and when initiated is often taken up by the other hen present.

Shaving baths may be taken during the period when two strange hens are together and have no relation either to posture or outcome except to be associated with an occasional "no contest". When one hen starts taking a shaving bath, the possible opponent often does too.

Quiet sitting occurs relatively more often than do some of the stances. It is not considered important in the posture picture, since a bird may sit from one stance and rise to the same one.

Analysis of Sample Contests

These contests are used as samples to illustrate the types of behaviour and relationships to the posture changes that occur in contests.

1. Leghorn vs. Rock: Rock added. Rock enters in "crouch." Leghorn "tall" avoids. Rock comes toward her. (Total time 5 seconds).

In this first sample contest, the Leghorn shows an immediate lack of aggressiveness, quickly avoids thus preventing actual contact.

2. Leghorn vs. Rhode Island Red: RIR added. Leghorn "crouched" in south end of pen; RI "crouched" in north, pecks shavings: Leghorn does likewise. RI goes toward south in "deep crouch"; Leghorn stands, gets "tall" and avoids to stand as RI gets close. (Time 5½ minutes).

Here the Leghorn changes stance during the contest. Her change occurs before the RI has threatened her or established physical contact.

3. Barred Plymouth Rock vs. Brahma: Brahma added. Brahma stands "crouched". Rock comes toward her in "crouch" and pecks twice before Brahma avoids "tall." (Time 2 seconds).

The Brahma hen, belonging to a notably unaggressive breed, maintains her aggressive posture until after she has been pecked. Here, the posture stance shows the extent of the Brahma's aggression.

4. New Hampshire vs. Rock: Rock added. NH "semi-crouched" in centre. Rock walks in "tall"; jumps to stand; jump down after 5 mins. 40 seconds, goes to centre and stands "tall". NH stands in "deep crouch". No contest. (Time 12 minutes).

There was no overt action in this contest to indicate the winner so it is listed as "no contest". The posture indicates the NH to be the winner. Some "no contests" appear to be conceded without action on the part of the contestants which seems to be true here. Other "no contests" are actually draws without pecking or fighting as when both birds have the same posture or oppose one type of crouch to another.

5. Rhode Island Red vs. New Hampshire: NH added. NH "semi-crouched" under door. RIR "semi-crouched" at opposite end. NH scratches and pecks shavings; RIR pecks shavings; they move closer together; 50 seconds NH runs across the distance and jumps on the RIR which fights back; many rounds occur (52 seconds) then NH avoids RIR. NH jumps to stand; is "crouched"; RIR pecks shavings; both make noise; after 4 minutes 25 seconds NH jumps down, scratches and pecks shavings in "crouch"; 6 minutes 10 seconds RIR attacks NH; they fight 15 seconds before NH avoids and is "tall." (Time 8 minutes 7 seconds).

This contest illustrates the usefulness of postures in finding that a contest has really ended. There was a temptation to remove the NH after her first avoid, although, judging from her behaviour she was not yet convinced of her loss. At the end, her assumption of "tall" stance indicated her decreased aggressiveness.

Discussion

The senior author, who was inexperienced at the time these contests were begun, attempted to sort criteria which could be used in accurate predictions of contest outcome. In time, from many criteria, the posture stances and their accessory actions were identified. Some posture phenomena had been observed (Potter, J., personal communication) but these had not been assembled in any systematic fashion and were classified more in terms of some accessory actions rather than the posture complexes themselves. We did not at the beginning of posture observations, know which postures were aggressive, but these became apparent as more contests were observed.

Other factors worked to our advantage in these observations: the relatively short time over which the contests were run, the long continued observations of a single population of hens in which very few individuals were added or removed over a two-year period and sufficient space to allow special contest pens to be set aside and which also allowed the observer to be close to "hen level".

Several aspects of these stances deserve detailed discussion. Morris (1956) discusses feather postures in birds and their physiological relationships. This author describes "sleeked", "relaxed", "fluffed" and "ruffled" feather postures. Our hens in postures "semi-crouch", "crouch", and "deep-crouch" exhibited only fluffed feathers but there was some variability in amount of fluffing between breeds, within a single breed and in the same individual in the same stance at different times. Some general trends were observed however, the greatest fluffing occurred in "deep crouch", and less fluffing in "crouch" or "semi-crouch". The fluffing in "deep crouch" is apparently not the amount of feather erection seen in preening or in

the sexual behaviour of Morris' finches and therefore is not "ruffling".

Morris (1956) also states that the physiological mechanism is due both to the sympathetic and parasympathetic nervous systems and that active birds "sleek" themselves for activity. This is supposedly to reduce the body temperature which will rise in activity. This is a most unusual physiological mechanism in activity since most adjustments, except increased secretion of epinephrine, are due to the production of metabolites and heat during activity. In mammals, the nerves causing piloerection are adrenergic and therefore increased secretion of epinephrine would cause piloerection. This, in fact, occurs in activity caused by fear or fighting. Obvious examples are dogs and cats under these conditions. The feather erection observed here in aggressive birds also shows this effect. Heat loss mechanisms should come into play only after activity has begun. Such mechanisms are parasympathetic and are exemplified by the panting and spreading of the wings of birds in long fights. Since very little data are actually available on the nervous reactions of birds, further explanations must await experimentation.

If one compares contest postures with those seen in the home hen flock, it is readily seen that only "crouch", "low" and tall" are seen in normal flocks and that in these conditions the predominant posture by far is "crouch". In testerosterone propionate-injected hens and in normal cocks, the predominant posture at all times is "semi-crouch". Since the dose levels in injected hens were very large (1 mg./day) and were above any physiological level, the effects of this substance must be considered to be at the drug level. Little is known about the effect of such drug levels on the central neıvous system but one suggested effect might be feather erection. This is pıobably not a direct effect but one mediated by the nervous system.

Since posture stances other than crouch are rarely seen in the flock, it is quite possible that the contest situation is a case of environmental stress. Environmental stress is defined as an unusual environmental condition to which the organism must make prompt internal adjustments to survive. Such environmental stressing agents as cold or heat are examples. Paired contests, fighting and unstable flock conditions might also be sources of environmental stress and might be correlated with similar physiological adjustments. Selye (1954) has listed many of the numerous internal adjustments which may occur including increased secretions of both the adrenal medulla and adrenal cortex. The ability of any species to make such adjustments and to maintain them over a period of time can determine the survivorship of the species. The numerous parameters used by Selye to determine stress should be applied to birds in the contest situation and such studies should be correlated with experiments on central nervous function before evaluations of the complicated behaviour patterns observed in postures are made.

Posture stances may be the best measure of aggressiveness yet devised since "tall" was correlated with losing and no-contest behaviour and it rarely preceded a win (22 wins in 2,474 stances). Similarly, "semi-crouch", crouch", and "deep crouch" were correlated with winning (2,448 winning stances, 6 losses and 266 preceding no contests). These facts, combined with the fact that birds tend to repeat their performance in contests (Foreman & Allee, unpublished data) make the domestic hen an extremely reliable form for studies on aggression.

Posture stances are also useful in flock recognition studies. Guhl & Ortman, (1953) state that they believed that hens which were introduced to flocks, either as strangers or as flock members which had been altered morphologically, behaved in a manner which betrayed their attitude to other flock members. This was true also when home flocks were transferred to new pens. However, posture *per se* may not be ıecognised because the "semi-crouch" of the TP injected flockmates did not produce continuous reactions by their flockmates. It is possible, however, that the period of comb growth and postuıe change was sufficiently prolonged that no loss of recognition or response to aggressive stance occurred. That such gradual conditioning to these changes did in fact occur, is shown by the introduction of a normal Ancona cock into a flock of Eberhard Leghorns two and one half months after the last injections of testosterone were given. This cock was soundly beaten in spite of his normal behaviour including cocky waltzing and initial wins over some of the hens. Thus other factors, such as recognition of the bird may in some conditions be more important than the posture stance displayed.

At this time, it should be made very clear that we do not know that posture is used by contestants in measuring the attitude of the opponent. That is to say, we do not know that posture in itself influences the outcome of a paired contest. It is a parameter that reveals to the

observer something of the attitude of the given bird. It is still possible that hens, which are keen enough observers to recognise one flockmate from another without extraneous marking devices, may recognise and take cues from the stances under normal conditions.

It is interesting to note briefly the similarity in behaviour of RIR and NH. Their incidence of fighting and waltzing is very similar and much higher than that shown by other breeds. The incidence of fighting makes it appear that these breeds, in our conditions, were not recognising each other as separate breeds. This point is emphasised by the work of Hale (1957) in which newly organised single- and mixed-breed flocks were studied. In these studies morphological modifications produced fighting more readily in the single breed flocks. The range of colour, size and shape among our NH apparently only added to the confusion, since they overlapped our very homogenous RIR (University of Illinois) in these characteristics. Further work should be done on these problems.

Summary

1. Six postures or stances observed in staged pair contests between common domestic hens are described.

2. We called them respectively "tall", "semi-crouch", "crouch", "deep crouch", "low", and "sex crouch."

3. All these stances except "deep crouch" may be observed in a flock with a cock present under various conditions.

4. "Crouch" is the usual posture that is characteristic of all hens in well organised flocks and found universally in flocks of long standing and in those having geometrical peck orders.

5. Postures called "tall", "low" and "sex crouch" are associated with the loss of a contest and may be given by submissive individuals in newly organised flocks, and, more rarely, in well organised flocks.

6. Postures called "semi-crouch", "crouch" and "deep crouch" are associated with winning in pair contests. "Deep crouch" has not yet been seen in organised flocks: "semi-crouch" may be associated with dominance under flock conditions.

7. Pecking on the floor, preening, flapping, sitting and clucking are mentioned briefly with reference to postures.

8. The postures described may be used as indicators of aggressiveness on the part of contestants in paired contests and in judging the conclusiveness of the outcome for the time being.

9. The posture data also indicate that most contests are decided soon after the birds are in the pen. These decisions are evidenced by the posture stances.

Acknowledgments

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REFERENCES

Allee, W. C. & Foreman, Darhl (1955). Effects of an androgen on dominance and subordinance in six common breeds of *Gallus gallus*. *Physiol. Zool.*, **28**, 89-115.

Guhl, A. M. & Ortman, (1953). Visual patterns in the recognition of individuals among chickens. *Condor*, **55**, 287-298.

Hale, E. B. (1957). Breed recognition in the social interactions of domestic fowl. *Behaviour*, **10**, 240-254.

Morris, D. (1956). The feather postures of birds and the problem of the origin of social signals. *Behaviour*, **9**, 75-113,

Potter, J. H. (1953). Personal communication.

Selye, H. (1954). Current trends in stress research. *Stress*, **4**, 39-100.

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THE EFFECT OF EARLY SOCIAL EXPERIENCE ON MALE SEXUAL BEHAVIOUR OF ANDROGEN INJECTED TURKEYS*

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A number of studies indicate that the degree of social experience may affect the expression of male sexual behaviour. However, the specific aspect of behaviour modified often is equivocal. Sexual behaviour may be described qualitatively in terms of motor *patterns* or measured quantitatively in terms of frequency or *levels* of expression. Further, the *stimuli* which elicit the behaviour may be described qualitatively or measured quantitatively in terms of their releasing value. Although the three components do not operate independently, each may be modified independently and in turn may or may not affect the expression of the others.

Beach (1958) with rats and Wood-Gush (1958a) with chickens found no differences in the percentage of isolated and socially reared individuals exhibiting completely organised sexual patterns on the very first trial. In contrast, Valenstein, Riss & Young (1955) observed deficiencies in the level of sexual behaviour of isolation reared male guinea pigs and concluded that the sexual behaviour of these animals had not been organised into an effective pattern. Similarly, fish reared in complete isolation exhibited a reduced level of sexual behaviour and aberrant mating patterns when compared to others raised with varying degrees of social experience (Shaw, 1957). Rosenblatt & Aronson (1958) indicated that the development of the mating pattern and level of behaviour of male cats depends upon sexual experience in combination with high androgen levels. In line with this thesis, the levels of sexual expression of isolation reared fish (Shaw, 1956) and chickens (Fisher & Hale, 1957) tended to increase upon repetitive testing.

With respect to the stimuli which release sexual behaviour of animals reared in isolation, the literature contains equally contradictory reports. Beach (1958) and Wood-Gush (1958a) found that such individuals (rats and chickens, respectively) react sexually to normal appropriate intraspecific stimuli, while Fisher & Hale (1957), Raber (1948) and Craig (1914) (chickens, turkeys and ring doves, respectively) reported that sexual responses of birds raised in isolation were directed to biologically inappropriate stimuli.

Some of the above differences may be attributed to species differences, while others may be engendered by differences in the degree of isolation. As Klopfer (1959) points out, external influences may be operative earlier than has been suspected, so that isolation starting as early as 1 day of age still may be quite different from isolation before birth or hatching. One also wonders whether part of the differences might lie in using levels as a measure of presence or absence of patterns, and the difficulty of determining optimal stimuli for isolated animals. In addition, disorientated behaviour might be interpreted as "aberrant patterns" when in fact a stimulus directing orientation simply is not present.

The object of the present study was to determine the effect of early social experience on the organisation of patterns of sexual behaviour, the stimuli releasing sexual behaviour, and the levels of sexual response.

Materials and Methods

Sexual behaviour was induced precociously in turkey poults by androgen injections. The feasibility of the technique was demonstrated by Hanford & Hale (1959) and has the advantage of providing data within a relatively short period of time. In addition the need for housing large birds in individual compartments for long periods of time is circumvented.

The experiments herein reported were first done by one author and then repeated by the other, with another group of birds. Since each worked independently, slight differences in techniques and testing routines were involved; hence, the designation "Trial 1" and "Trial 2" will be used where appropriate.

Hatching.

Trials 1 *and* 2. Four days before expected hatching, incubating White Holland turkey eggs were covered with aluminum containers in a

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manner permitting free circulation of air around each egg, yet providing complete visual and tactile isolation of each hatchling. Poults were banded for individual identification within three to four hours after hatching, and transported in individual closed containers to randomly determined places in the brooder boxes.

Brooding

Trials 1 *and* 2. Eight brooding sections 5 ft. × 1 ft. × 10 in. high, were used. Four of the eight sections were partitioned into 1 ft. × 1 ft. × 10 in. compartments, each housing one bird. (Fig. 1 illustrates the two types of brooder compartments.) Thus there were initially 20 birds in individual compartments and four groups of 5 birds each in the remaining compartments (except for one group of 10 birds in Trial 1).

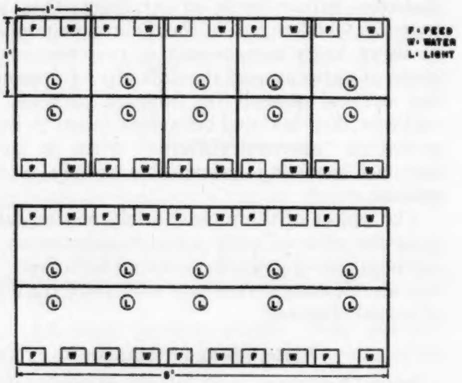


Fig. 1. Diagram of the "isolation" (upper) and "group" (lower) boxes used for brooding, as viewed from above.

Heat necessary for brooding was provided continuously by a naked light bulb, and food and water were available *ad libitum* for each bird. Visual isolation was obtained by using solid ½ in. plywood partitions. The tops and bottoms of the boxes were constructed of ½ in. mesh hardware cloth in order to accustom the birds to the observer. However, visual isolation was maintained when birds were removed for injection or testing by temporarily covering all boxes with plywood. It should be emphasised that "isolation", as used in this report, is only with respect to visual and tactual stimulation from other birds.

Injections

Precocious male sexual behaviour was induced by daily injections of 1 mg. testosterone propionate (Schering's Oreton). In Trial 1, injections were administered intramuscularly into the thigh region from the 6th through 35th day of age. In Trial 2, injections were administered subcutaneously into the neck region, from the 7th day of age until the animal was killed.

Treatments

In order to study the effect of different social experiences the birds were either: (1) grouped, (2) grouped and then isolated, or (3) isolated. Minor variations from these treatments are noted below.

Trial 1. (38 surviving birds).

Grouped: 15 birds remained in small groups for the 32-day experimental period;

Group-isolated: 5 birds were moved from the initial 10-bird group to individual isolation compartments at 10 days of age and the other 5 at 20 days of age;

Isolated: 8 birds remained in isolation compartments for the 32-day experimental period; 5 others were moved from isolation to group compartments at 20 days of age.

At 32 days of age, all birds were removed from their compartments and released together into a 12 ft. × 10 ft. community pen. The genetic sex of each bird was determined on the basis of morphological characteristics at sexual maturity or by autopsy of those birds that died before reaching maturity.

Trial 2. (31 surviving birds).

Grouped: 13 birds remained in small groups for the entire experimental period;

Group-isolated: 6 birds were moved from group to isolation compartments at 11 days of age;

Isolated: 8 birds remained in isolation compartments for the entire experimental period;

Supplementary: 4 birds, in irregular categories, were observed but are not included in the data.

At the end of the testing routine, birds were sacrificed and sexed by gross anatomical examination.

Test Models

Previous studies on domestic turkeys (Schein & Hale, 1957, 1958a) indicated that a dummy female's head alone serves as an adequate arousal stimulus for normally reared, sexually active males. Some 3-week-old, androgen in-

jected, turkeys strutted and displayed to a dummy head in adult-like fashion (Schein & Hale, 1958b). On the basis of these and other observations, the following objects were used as sexual releasers for both Trials.

Poult head: a poult of approximately the same age as the experimental birds was killed and stuffed with cotton. The head was removed and mounted on a stiff wire base so that it could be presented separately in an upright position;.

Poult body: the stuffed body of the killed poult, presented without a head.

Human hand: the observer's hand placed on the floor of the test box, palm up (Trial 1) or down (Trial 2). A hand was used since it is possible that some of the animals became imprinted to the observer during the course of the experiment.

Inanimate objects: a small wooden block, an unlit lightbulb, or an inverted feed cup.

Behaviour and Testing Procedures

Responses

In both Trials 1 and 2, responses of the poults to the introduced stimuli were classified as follows:

Escape, the bird tried to escape from its box when the stimulus object was present;

Avoidance, the poult avoided the stimulus object but made no effort to escape from the box;

No Response, avoidance was reduced to zero, and the bird showed no evidence of sexual behaviour;

Strutting, courtship display similar to that shown by sexually active adult males;

Copulatory movements, the poult "mounted" and "trod" the model in adult-like fashion; poults presented with a head trod the area immediately around the head, pressing the breast against the model.

Testing Procedure

Trial 1. Testing was done in the bird's home environment. Thus, the isolated poults were tested singly in their own boxes, while the grouped ones were tested collectively in their group box. Collective testing has previously been used satisfactorily with chickens (Fisher & Hale, 1957).

Qualitative tests: responses scored in terms of escape, avoidance, no response, strutting, or copulatory movements as noted above.

Single stimulus: head.

First, Age 17-18 days. All birds were confronted with a dummy head for at least a 5-minute period or until "mounting" occurred.

Second, Age 23-24 days. All birds were presented a dummy head combined with the dummy body for at least a 5-minute period or until "mounting" occurred. However, there was no evidence that the presence of the body modified the results, so this test was treated as a head test in the analysis.

Preference: head, body, and hand.

Age 35 days. Three days after the birds had been grouped together in a community pen, each was tested in the same pen in the absence of its penmates. In this test, the head, body and hand were placed on the floor of the pen approximately 2 ft. apart at the points of an imaginary equilateral triangle. The bird was released in the middle of the triangle and its behaviour noted for at least 5 minutes or until "mounting" occurred. In the event of a sexual response to one stimulus object, an effort was made to transfer the response to the other stimuli. For example, if a bird made copulatory movements to the hand, the hand was moved slowly to the head and to the body, and then away again. However, in no case was it possible to transfer the response from one stimulus to the other.

Trial 2. All birds were tested individually in 2 ft. × 2 ft. × 1 ft. boxes except for a few limited tests with three poults (Nos. 230, 241, 250) at 19 days of age in their home box.

Qualitative tests: responses scored as in Trial 1.

Single stimulus: head, body or hand.

First, Age 32-35 days. Poults were placed in the test boxes 1 to 12 hours before testing. All birds were tested for 5 minutes with each model. Three birds, one from each treatment category, were tested at the same time in adjoining test boxes (in so far as numbers permitted), with presentation of the three stimulus objects counterbalanced.

Second, Age 40-43 days. In order to determine the repeatability of the initial test in Trial 2 and to measure any changes in behaviour, 1-minute tests were given to all birds except for grouped females. Birds were placed in the test boxes immediately prior to testing. Poults were tested as in the first test but with presentation of the stimuli in a different sequence, for a given bird, than in the initial tests. In the interval between the first and second tests, the poults had been given short tests with several other live poults.

In addition to tests with the usual stimulus objects, five of the grouped poults and all other birds also were given 1-minute tests with the inanimate objects.

Quantitative tests: scored in terms of the amount of time spent in sexual activity.

Single stimulus: head, body or hand.

Age 50-56 days. In the qualitative tests some birds reacted to several stimulus objects. In order to evaluate the relative stimulus value of the various objects for these birds, quantitative tests were carried out with several males. Tests of 5 minutes duration each were given with head, body and hand, starting when the poults were 50 days old. To obtain maximum response levels, all birds were maintained in isolation for at least seven days before the testing started. Only one test was given per day and each bird was tested at least twice with each stimulus object. The total time spent in strutting or copulatory movements was determined by recording the activity of the bird during successive 5-second periods. These were summed to give the total activity during the 5-minute test. The one test per day procedure was adopted since a rapid response decrement had been observed in sequential tests.

Paired contests with other poults: At various times following the initial test, poults were tested in brief paired contests with other poults. These included pairings with both strutting poults and threatening or attacking poults.

Results

Data on all birds used in both Trials are presented in Table I. The birds within each treatment category are listed by genetic sex, and individual poults are arranged in approximate order from the most to the least sexually reactive. Birds in Trial 1 are numbered in the 100 series, and those in Trial 2 in the 200 series.

During the normal course of feeding, watering and injecting, many individuals were observed casually to strut in the absence of specifically presented stimuli. Isolated birds strutted openly in the presence of the observer, while grouped birds more often were observed covertly (usually, all except the most reactive grouped birds stopped strutting and exhibited avoidance when the observer was in view). Strutting behaviour was observed for the first time in a few birds as early as four days after the injections were started. Birds displaying in the absence of specifically presented stimuli are listed in Column 2 of Table I in order to provide an estimate of the potential population of sexually responding poults. Some birds were seen strutting often, others only rarely.

Qualitatively, the reaction of a bird to a stimulus situation was generally consistent from test to test. Birds responding sexually in one test tended to respond sexually in most or all of the test situations. Others were similarly consistent in avoiding or in not responding to the stimulus objects. Identical results were obtained on the first and second tests in 52 per cent. of the 69 tests in Trial 2, while 38 per cent. differed by only one response classification. Only seven pairs of results differed by more than one response classification: one group-isolated female (260) accounted for three of the differences, and three grouped birds were represented in the other four differences. The grouped poults were the most variable, while group-isolated and isolated males were quite stable and gave identical results in 83 per cent. of the tests.

Patterns of Behaviour

Prior to the initial test and during their first test with the various stimulus objects, at least some poults in each treatment category were seen to display. In both sexes the display pattern (Plate I) was similar to adult male courtship display in that the neck was held in a tight "S" shape, head close to the body, snood elongated, back feathers raised and fluffed, wing feathers spread and drooped slightly, and the tail raised, fanned and angled toward the stimulus object.

Upon the presentation of appropriate stimuli during the initial test, fully organised copulatory patterns were exhibited by some birds in the isolated and group-isolated categories, but not in the grouped category. In all instances the copulatory movements (Plate I) were miniature replicas of adult patterns and included mounting, treading and trampling the models, and lowering the tail with a quivering motion. Copulatory patterns exhibited by individuals in their first test situation were not visibly different from those exhibited in subsequent tests.

There was no evidence of a gradual maturation of sexual behaviour with repetitive testing. *A priori*, the probability would appear greater that repeated testing might contribute more to the organisation of sexual behaviour in the isolated and group-isolated poults rather than in the grouped ones. Nevertheless, seven of the males in the former categories exhibited copulatory behaviour during initial tests with an appropriate model and only two of the remain-

PLATE I

Androgen-injected poult making copulatory movements on a dummy model; another poult struts nearby.

Table I. Responses of Poults to Various Stimulus Objects.
(Legend: – – = Escape; – = Avoidance; O = No Response; S = Strutting; C = Copulatory Movements)

Bird no.	Strutting Non-test	Head test First	Head test Second	Body test First	Body test Second	Hand test First	Hand test Second	Preference test
Grouped Poults								
males								
249	often	S	O(C)***	S	O(S)	–	–(S)	
250	often	S	O(C)	S	O(S)	S	O(S)	
182	often	S	–					–
176	often	S	–					–
251	often	– –	–(C)	– –	– –(S)	S	–(S)	
189	often	–	–					–
187	rare	–	–					–
257		– –	O	– –	O	– –	–	
females								
247	rare	O	S	O	S	–	S	
188	rare	–	–					O
186	rare	–	–					O
246		O	O	O	O	–	–	
248		O	O	O	O	–	– –	
255		O	O	O	O	– –	–	
254		O		–		– –		
256		O		O		– –		
253		–	–	O	–	– –	– –	
245		–		–		– –		
252		– –		–		– –		
Also 9 females (Trial 1) which consistently avoided.								
Group-Isolated Poults								
males								
243	often	C	C(C)	C	C(C)	S	S(S)	
262	often	C	C(C)	C	C(C)	S	S(S)	
155	often	C	C					C to head
158*	often	S*	C					C to head
168	rare	C	C					C to head
167	rare	C	C					C to head
152*		–*	– –					–
females								
164		C	C					C to head
160*		–*	S					C to hand
261		S	O	S	S	O	S	
258		O	O	C	C	–	O	
260		–	C	–	S	–	S	
159*	rare	–*	O					O
259	rare	–	O	O	O	O	S	
163		O	O					–
170*		–*	O					–
Isolated Poults								
males								
157	often	C	C					C to hand
228	often	S	S(S)	S	C(C)	C	C(C)	
241	often	S	S(S)	S	S(S)	S	S(S)	
166	often	– –	– –					C to hand
153	often	– –	S					S to hand
230	often	–	O(–)	–	–(–)	S	S(S)	
156	rare	– –	– –					S to hand
225	rare	–	–	–	–	–	–	
175**	rare	– –						O
286		–	–	– –	–	– –	– –	
240		– –	– –	– –	–	– –	– –	
females								
171**	often	C						C to hand
151	rare	S	S					S to hand
169	often	– –	S					S to hand
154	often	– –	– –					S to hand
165	rare	– –	O					O
172**		– –						–
239		– –	–	–	– –	– –	–	
232		–	– –	– –	– –	– –	–	
173**		– –						O
174**		– –						O

* Isolated at 20 days of age; first test made under group conditions.
** Grouped at 20 days of age.
*** Response in parenthesis refers to qualitative results in quantitative test, Trial 2.

ing males (158, 166) in these categories showed this behaviour for the first time in later tests. Of five other poults which exhibited copulatory behaviour for the first time in later tests, three were grouped males and two were group-isolated females.

On rare occasions dramatic transitions in behaviour were observed over a period of seconds. One poult in a supplementary category avoided a head model for two minutes, then approached it without strutting and abruptly started copulatory movements which continued for three minutes. Another tried to escape for more than 4 minutes and suddenly moved to a dummy body in courtship display.

Intromission was precluded by the nature of the models, and actual mounting could not occur when the head model was used. Variations in effective neuromuscular co-ordination of copulatory patterns were not assessed. Actually, the effectiveness of normally reared adult males in completing copulations is so variable that a rather large population would be necessary to establish minor treatment differences (Hale, 1955).

Stimuli Releasing Behaviour Patterns

Rearing conditions up to 10 days of age had a marked effect in determining the stimuli which released sexual behaviour. Responses of isolated birds in the Preference test were all to the observer's hand. In contrast, all but one of the reacting group-reared birds responded to the head model. None of the poults in any treatment category reacted to the body in the Preference test. However, under single stimulus test conditions in Trial 2 the body model did provide some sexual stimulation.

Only those poults responding sexually in at least one test situation serve to delineate the effective stimuli. Six grouped, 12 group-isolated, and 11 isolated poults fit this criterion. Stimuli releasing sexual behaviour in these poults are shown in Fig. 2. Since not all poults were tested with each model, the numbers of birds involved are noted under each stimulus object. Data are presented in terms of the percentage of tested poults responding to a given model. For example, 6 of the 12 group-isolated birds were tested with the body. Of these, 3 (50 per cent.) exhibited copulatory movements, and two additional poults strutted, making a total of 5 (83 per cent.) exhibiting sexual responses.

Trends in the quantitative test for those poults reacting to all three models were very similar to

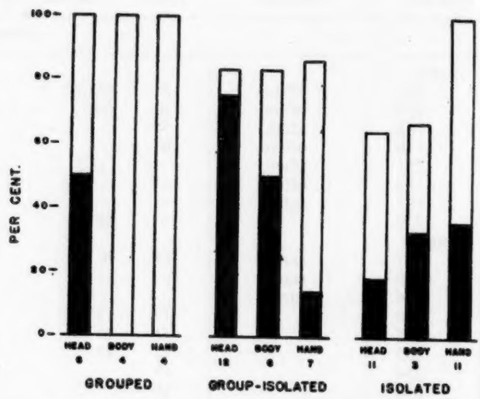


Fig. 2. Percentage of sexually reactive poults exhibiting sexual responses to a given model (copulatory movements in black, strutting in white). The number of birds involved is indicated under each model.

the qualitative observations presented in Fig. 2. The quantitative data are presented in Fig. 3 for three grouped (249, 250, 251), two group-isolated (243, 262) and two isolated (228, 241) poults.

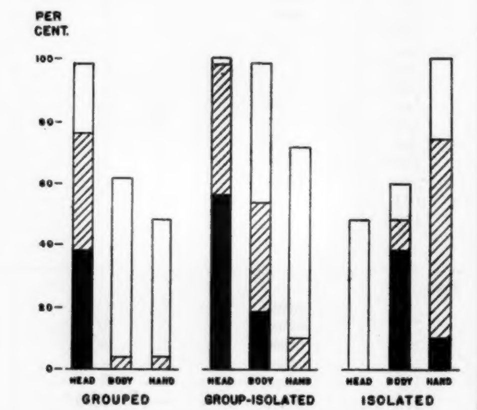


Fig. 3. Percentage of time during 5-min. quantitative tests in which poults exhibited copulatory movements (black), mounted or pressed against model (cross hatch) or strutted (white) in response to various models.

Test scores were computed for the quantitative tests by multiplying the time spent exhibiting copulatory movements by two and adding this to the time engaged in all aspects of sexual behaviour. Thus a bird attempting copulation for the full 5-minute period was scored $(5 \times 2) +$

5 = 15, and one strutting the entire period scored $(0 \times 2) + 5 = 5$. Observed scores ranged from 0 to 15 and the correlation between scores on the two quantitative tests with the same model was 0·90. Thus the high reliability of this test recommends its use for more extensive measurements of the variability of releasing stimuli in experimental populations.

Some isolated (157, 228, 241) and group-isolated (243, 260) poults, but no grouped poults, displayed to inanimate objects as well as the usual test models. However, only Nos. 157 and 243 attempted copulation with such objects: by the former in response to a rubber ball, an unlit light bulb, and a wooden block, and by the latter to the wooden block and the light bulb.

Levels of Sexual Behaviour

Sex differences in sensitivity to the hormone were readily apparent. In the non-test observations 85 per cent. of the males in contrast to only 26 per cent. of the females were observed in courtship display. During the various tests, 46 per cent. of the males attempted copulation as compared with only 13 per cent. of the females.

The frequency or level of sexual responses to appropriate stimuli might have been modified through experience (as were the effective stimuli) even though the motor patterns were not affected. Results summarised in Table I clearly indicate over all differences in *apparent* levels of response for birds in the various treatment categories. Not only did a greater percentage of group-isolated poults respond sexually, but the frequency of "copulatory" behaviour was markedly higher than in any other group. Under the test conditions of this experiment, the rating for levels of sexual behaviour as determined from an inspection of Table I would be, from highest to lowest: group-isolated, isolated, grouped.

However, it should be re-emphasised that isolated and group-isolated birds were maintained in individual quarters while grouped poults were in contact with other poults (or at best separated for a few hours) prior to testing. When three grouped poults (249, 250, 251) were isolated for one week prior to the quantitative tests, levels of response increased sharply and were comparable to the most reactive birds in other categories.

Evidence of a marked response decrement in the continued presence of stimulus objects was obtained by subjecting two group-isolated poults (243, 262) to continuous testing for more than 30 minutes (Fig. 4). Each model was presented for 5 minutes, removed and another introduced. The number of minutes during which various aspects of sexual behaviour were exhibited is indicated for each successive 5-minute period. These poults were predominantly head reactors

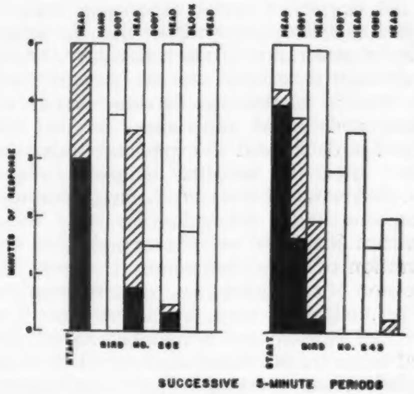


Fig. 4. Response decrement during continuous testing with various models (legend same as in Fig. 3).

and it will be noted that although there was usually an increment in sexual behaviour each time the head was introduced, the response was considerably less than that observed during the previous head presentation. Similar decrements were observed with other poults during the routine 5-minute quantitative tests.

Relationship of Aggression to Levels of Sexual Behaviour

In tests with other poults, grouped and group-isolated males gave the courtship display and continued to strut even when attacked by other birds, except that occasionally one of the less sexually reactive males would stop strutting and return the attack. Females in these treatment categories attacked introduced poults so consistently that fighting behaviour was a fairly reliable indication of the sex of the bird. After initial threats some of these females appeared to give a sexual crouch. Thus, those birds with the lowest male sex drive were most prone to show aggressive behaviour.

Wood-Gush (1958a, 1958b) observed an inverse relationship between aggressive and mating behaviour in sexually-inexperienced cocks. He suggested that this may mean that the aggressive drive masks the sexual drive, or that aggressive behaviour is aroused because sex drives are only

weakly activated. Results with the poults in the present study support the second interpretation.

Discussion

An observed relationship between a behaviour and the degree of social experience often is accepted as *prima facie* evidence that the organisation or maturation of the behaviour is modified through experience. In the present study there was a relationship between sexual behaviour and social experience, in that the grouped birds showed less apparent sexual behaviour than the isolated or group-isolated birds. Following the line of reasoning mentioned above, one might conclude that early social experience *interfered* with the organisation and maturation of sexual behaviour. However, the expression of sexual behaviour in test situations may be modified strongly by factors other than the actual capacity for sexual behaviour. The actual capacity, or basic sexual potential of the population, is represented in Fig. 5. The diagram is an hypothetical representation of the frequency distribution of male sexual behaviour in males and females receiving a maximal dose of androgens, and is inferred from results described by Davis & Domm (1943), Beach (1948) and Hanford & Hale (1959).

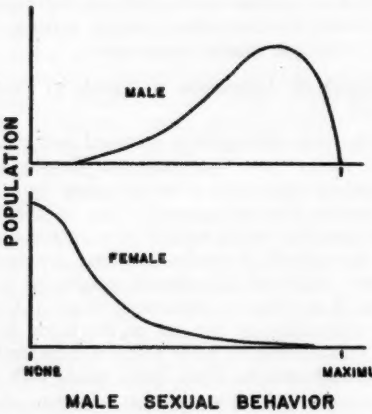


Fig. 5.

Three factors modifying the expression of sexual potential are: (1) avoidance; (2) transient effects of continuous stimulation on response potential; and (3) the appropriateness of the stimulus presented. A conceptual model based on these three factors is adequate to predict in a general way the behaviour of all birds used in this experiment. The effect of these factors on the expression of the basic sexual potential of the population is discussed below in terms of the conceptual model.

Avoidance. A primary assumption in the conceptual model is that escape-avoidance behaviour and sexual behaviour are *not* extremes on a single continuum. However, escape-avoidance completely masks sexual behaviour, and must be reduced to zero before the expression of sexual behaviour can occur. If all animals avoided, there would be no overt expression of sexual behaviour although the basic sexual potential of the population would be unchanged. If avoidance were reduced by 50 per cent., then those animals in the unshaded portion of Fig. 6, representing *all* levels of responses, would show sexual responses, while the others would continue to avoid. Thus, an increase or decrease in the degree of avoidance would respectively decrease or increase the *number* of animals responding, but would not affect the *levels* of sexual responses of those birds which do respond.

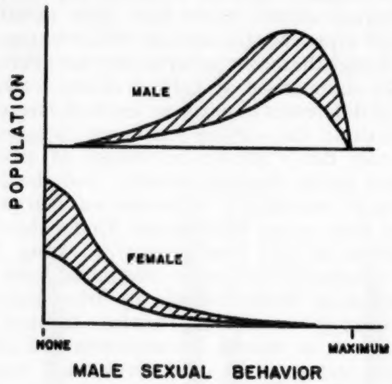


Fig. 6.

The conceptual model contrasts with the concept of a balance between competing drives (Miller, 1944) which has been used so successfully in open field approach-avoidance situations. Use of the concept of balanced drives leads to a very different interpretation of the relationship between the masking effect of avoidance behaviour and the basic sexual potential of the population. Specifically, it implies that if avoidance is reduced by 50 per cent., sexual behaviour will be expressed only by those individuals with

higher basic potentials (unshaded areas in Fig. 7), while those with lower potentials would continue to avoid (shaded areas). The concept of balance fails to explain certain aspects of the

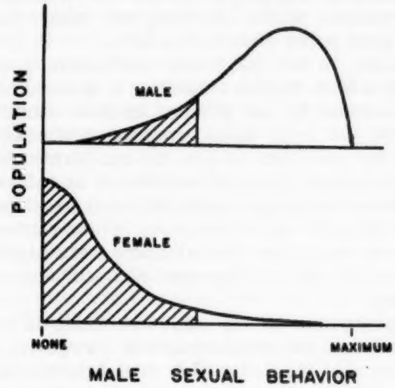


Fig. 7.

data in this experiment which are adequately accounted for in the conceptual model. The distinction between the two approaches is considered crucial in the interpretation of experimental findings.

Transient Effects of Continuous Stimulation. This effect has been noted previously (Fig. 4 and attendant text) and is schematically presented in Fig. 8. A given stimulus is most effective at the initial time of presentation, and its effectiveness is markedly reduced during con-

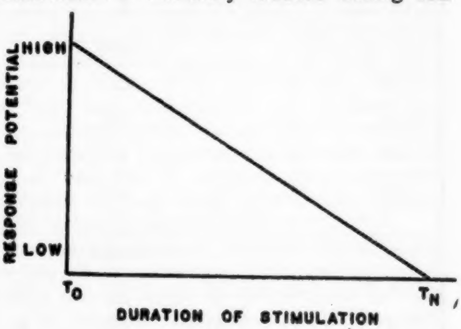


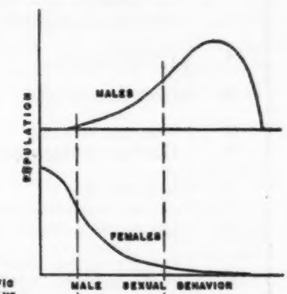
Fig. 8.

tinuous presentation. Thus, an evaluation of the temporary response potential is essential for a valid analysis of the data.

Appropriateness of the Stimulus. It has been noted previously (see Stimuli Releasing Behaviour Patterns in Results) that the effectiveness of a stimulus was strongly modified by early rearing conditions. Thus, the stimulus value of a given model is not identical for all birds, and the difference must be taken into consideration in any critical examination of the data.

Evaluation of the Data in Terms of the Conceptual Model. At this point we may go back and revaluate the data in Table I. As noted above, the avoidance evoking characteristics of the test situation affects the numbers of birds avoiding but does not affect the level of response of sexually reacting birds. Therefore those cases where avoidance occurred in a test may be ignored in considering the effect of treatments on levels of sexual behaviour. Only the other two factors, transient effects of continuous stimulation and appropriateness of the stimulus, affect the level of sexual response.

To illustrate, we may designate levels of response on the continuum of male sexual behaviour (Fig. 5) in terms of no response (0), strutting (S), and copulatory movements (C). Four hypothetical test conditions (A, B, C, D) taking into account response potentials and specific releasing stimuli are listed in Fig. 9. Test condition A represents a population in an



CONDITION	RESPONSE POTENTIAL	SPECIFIC STIMULUS	MALE	SEXUAL	BEHAVIOR
A	HIGH	PRESENT	0	S	C
B	HIGH	ABSENT	0	0	S
C	LOW	PRESENT	0	0	S
D	LOW	ABSENT	0	0	0

Fig. 9.

optimal test situation. Note that either a low response potential or the absence of an appropriate stimulus shifts the continuum to a lower level of male sexual behaviour (B or C). A deficiency of both at the same time shifts the continuum even further, to the point where no male sexual behaviour is evident (D).

The various tests that were used actually involved very different conditions depending upon

interaction between treatment categories and test situations. Therefore, the relevant data in Table I have been reassembled and listed in Table II in terms of test conditions represented by the various test situations. Test conditions

Table II. Effect of Test Conditions on Level of Sexual Behaviour.

Test condition*	Test situation	No. of tests in which poults reponded with:					
		O	S	C	O	S	C
	Grouped birds	males			females		
A	Quantitative test, head	0	0	6			
B	Quantitative test, hand	0	6	0			
C	Non-test strutting	1	7	–	17	3	–
C	Qualitative test, head	3	4	0	9	1	0
C	Preference test				2	0	0
D	Qualitative test, hand	1	2	0	0	1	0
	Group-isolated birds						
A	Quantitative test, head	0	0	4			
A	Qualitative test, head	0	1	11	8	2	3
A	Preference test	0	0	4	1	0	2
B	Quantitative test, hand	0	4	0			
B	Non-test strutting	1	6	–	7	2	–
B	Qualitative test, hand	0	4	0	3	3	0
	Isolated birds						
A	Quantitative test, hand	0	4	2			
A	Qualitative test, hand	0	4	2			
A	Preference test	1	2	2	3	3	1
B	Quantitative test, head	0	4	0			
B	Non-test strutting	2	9	–	5	5	–
B	Qualitative test, head	1	5	2	1	3	1

*See text and Fig. 9.

were specified as follows: predominately head reacting birds (grouped, group-isolated) were classed as "stimulus present" in head tests and "stimulus absent" in hand tests; the converse held for hand reacting poults (isolated). In non-test strutting, grouped birds were classed as "stimulus present" (sexual stimulation provided by group mates) and group-isolated and isolated birds as "stimulus absent." Response potential was classified as "low" for the grouped birds since they were housed continuously in the presence of sexual stimulation provided by other poults. Response potential was classed as "high" for isolated and group-isolated poults, and for the grouped poults following one week's isolation prior to the quantitative tests.

Hence, in the qualitative head tests, group-isolated birds were in condition A, isolated birds in condition B, and grouped birds in condition C. On the other hand, grouped birds (which were in condition C for the qualitative head tests) changed to condition A for the quantitative head test resulting in a decided shift to a higher level of male sexual behaviour. These examples serve to emphasise that identical test situations do not necessarily represent identical test conditions.

Examination of the trends in Table II both within and between treatment categories indicates that the conceptual model presented in Fig. 9 has rather high predictive value with respect to the levels of response. In Table III the data are summarised in terms of the percentage distribution of sexual responses for the four test conditions without regard to treatment categories. The model adequately predicts the distribution of behaviour in all instances (except

Table III. Distribution (percentage) of Sexual Responses for the Test Conditions Without Regard to Treatment Categories.

Test condition*	No. of tests	Response		
		O	S	C
		males		
A	43	2	$\underline{26}$	$\underline{\underline{72}}$
B	44	$\underline{9}$	$\underline{\underline{86}}$	5
C	15	$\underline{27}$	$\underline{\underline{73}}$	0
D	3	$\underline{\underline{33}}$	67	0
		females		
A	23	$\underline{\underline{52}}$	$\underline{22}$	$\underline{26}$
B	30	$\underline{\underline{53}}$	$\underline{43}$	4
C	32	$\underline{\underline{87}}$	$\underline{13}$	0
D	1	$\underline{\underline{0}}$	100	0

= Predicted predominate behaviour.
— Predicted to occur but at a lower frequency.
*See text and Fig. 9.

perhaps under condition D, where the number of tests is exceptionally small). These results strongly suggest that *transient test conditions* rather than *prolonged differential social experiences* are the primary factors contributing to the behavioural results presented in Table I.

One deviation of note is that under test condition A the isolated male poults showed a lower level of sexual response than those in the other treatment categories (Table II). However, it is not possible to state conclusively that isolated poults are deficient in sexual behaviour, since at present there is no way to compare the relative stimulus value of the hand for isolated poults with the head for grouped poults. The fact that isolated poults reacted to a broader spectrum of stimuli with less differentiation (Figs. 2 and 3) lends support to the possibility that the hand is not an optimal stimulus. Therefore, it may be that the three test situations labelled "condition A" for the isolated poults (Table II) should be intermediate between A and B. Hence, the deviation mentioned above might be the result of a sub-optimal test condition rather than a lower level of sexual expression.

The importance of the stimulus as a variable in measuring development of behaviour has frequently been ignored. In another context Hale & Almquist (1956) and Fisher (1958) have indicated that the level of sexual responses may be modified markedly by manipulation of stimulus conditions.

Stimulus specificity was most apparent in the grouped birds, which restricted copulatory movements to the head model and only strutted to the other stimuli. In this respect, their behaviour conforms to that of normally-reared adult males (Schein & Hale, 1957, 1958a). Less stimulus specificity was evidenced by the isolated and group-isolated birds, which gave copulatory movements to a wider range of stimulus objects. Indeed, one bird in each of these categories attempted matings with light bulbs, wooden blocks, upturned feeders, and a rubber ball.

The marked contrast between the apparent diversity of the results on first examination of Table I and the highly uniform results in Table II again suggests that many of the divergent results reported in the literature with various species may reflect differential test conditions rather than differential effects of experience. As noted in the foregoing discussion, standardised test situations may not represent the same test conditions for animals with different social experience.

Tests for the presence of organised patterns of behaviour demand optimal conditions for expression of sexual response, which are stated more readily than achieved. With isolated individuals the problem of reducing avoidance on the first test to a point which permits a true evaluation of sexual behaviour for all individuals in the experimental population may be impossible to resolve. In the present study the confined test area tended to trigger either sexual or avoidance behaviour almost immediately. Avoidance or strutting behaviour was typically exhibited within seconds, and copulatory movements usually started within half a minute. In a larger open field type testing area, avoidance behaviour might be expressed by distance with no overt expression of either avoidance or sexual behaviour. As familiarity with the test situation increases during prolonged testing, the actual avoidance distance might be decreased and accompanied by an increase in the expression of sexual behaviour. Thus an increase in sexual behaviour scores with repetitive or prolonged testing in an open field type situation may reflect a decrease in fear responses rather than maturation or organisation of sexual behaviour.

It is noteworthy that minor differences in techniques, including age at testing, mode of hormone administration, position of the observer's hand during a test, individual versus collective testing, or experience with other poults between tests did not influence the trend of the results.

Summary

The object of this study was to determine the effect of early social experience on the patterns and levels of sexual behaviour and on the stimuli releasing sexual patterns. Androgen injected male and female turkeys were studied from hatching through 5-8 weeks of age. Twenty-eight birds lived in grouped environments, while 21 others were reared under conditions of intraspecific visual isolation. Sixteen additional birds were raised in groups for a period of time post-hatching, and then visually isolated for the duration of the experiment. Various stimulus objects were used as sexual releasers in several tests during the experiment. These included a poult head, a poult body without the head, the observer's hand, and several inanimate objects.

Complete strutting patterns were exhibited by some birds in each treatment category prior to or during their first test. Of 8 males in the isolated and group-isolated categories which

showed fully organised "copulatory movements" at some time during the experimental period, 7 did so during their first test with an appropriate stimulus. Further, the sexual reaction of a bird to a particular stimulus object generally was consistent and did not increase in repeated tests during the course of the experiment. Hence, it is concluded that the development of the pattern of sexual behaviour is not dependent upon early social or sexual experience.

Treatment differences were most notable with respect to the stimuli which released sexual behaviour. In a preference test, no bird in any treatment category responded preferentially to the headless body. Those birds with early group experience reacted predominantly to the head model, which is in accord with what has been observed in normally reared adult males. However, birds reared in isolation gave sexual responses predominantly to the observer's hand. Hence, it is concluded that early social experience markedly modifies the releasing value of sexual stimuli.

Under the test conditions of this experiment, ratings for levels of apparent sexual behaviour would be, from highest to lowest: group-isolated, isolated and grouped birds. However, it is pointed out that expression of the sexual potential of the population is dependent upon: (1) avoidance behaviour; (2) the appropriateness of the stimulus; (3) the temporary response potential resulting from the degree of recent stimulation. The data were re-evaluated in terms of a conceptual model which incorporated only these factors and the sex differences in sensitivity to androgen injections. Application of the model to the data strongly suggests that transient test conditions rather than prolonged differential social or sexual experiences contributed to the apparent differences in levels of response.

REFERENCES

Beach, F. A. (1948). *Hormones and behaviour*. New York and London: Paul B. Hoeber, 368 pp.

Beach, F. A. (1958). Normal sexual behaviour in male rats isolated at fourteen days of age. *J. comp. physiol. Psychol.*, **51**, 37-38.

Craig, W. (1914). Male doves reared in isolation. *J. anim. Behav.*, **4**, 121-133.

Davis, D. E. & Domm, L. V. (1943). The influence of hormones on the sexual behaviour of domestic fowl. From *Essays in Biology*, Univ. of California Press, pp. 171-181.

Fisher, A. E. (1958). Effects of stimulus variation on sexual satiation in the male rat. *Amer. Psychol.*, **13**, 382 (abst.).

Fisher, A. E. & Hale, E. B. (1957). Stimulus determinants of sexual and aggressive behaviour in male domestic fowl. *Behaviour*, **10**, 309-323.

Hale, E. B. (1955). Defects in sexual behaviour as factors affecting fertility in turkeys. *Poult. Sci.*, **34**, 1059—1067.

Hale, E. B. & Almquist, J. O. (1956). Effect of changes in the stimulus field on responsiveness of bulls to a constant stimulus animal. *Anat. Rec.*, **125**, 607 (abst.).

Hanford, P. V. & Hale, E. B. (1959). Unpublished data.

Klopfer, P. H. (1959). An analysis of learning in young anatidae. *Ecology*, **40**, 90-102.

Miller, N. E. (1944). Experimental studies of conflict. In Hunt, J. McV., *Personality and behaviour disorders*. New York: Ronald Press.

Raber, H. (1948). Analyse des Balzverhaltens eines domestizieren Truthans (*Meleagris*). *Behaviour*, **1**, 237-267.

Rosenblatt, J. S. & Aronson, L. R. (1958). The influence of experience on the behavioural effects of androgen in prepuberally castrated male cats. *Anim. Behav.*, **6**, 171-182.

Schein, M. W. & Hale, E. B. (1957). The head as a stimulus for orientation and arousal of sexual behaviour of male turkeys. *Anat. Rec.*, **128**, 617-618 (abst.).

Schein, M. W. & Hale, E. B. (1958a). Stimuli releasing sexual behaviour of domestic turkeys. 16mm. Film, Psychological Cinema Register, PCR-114K, Pennsylvania State Univ.

Schein, M. W. & Hale, E. B. (1958b). Stimuli releasing sexual behaviour of turkeys. *Poult. Sci.*, **37**, 1240 (abst.).

Shaw, Evelyn (1956). Sexual behaviour of male platyfish raised in individual aquaria. *Anat. Rec.*, **125**, 606 (abst.).

Shaw, Evelyn (1957). Sexual behaviour of male platyfish reared in altered environments. *Anat. Rec.*, **128**, 621 (abst.).

Valenstein, E. S., Riss, W. & Young, W. C. (1955). Experiential and genetic factors in the organisation of sexual behaviour in male guinea pigs. *J. comp. physiol. Psych.*, **48**, 397-403.

Wood-Gush, D. G. M. (1958a). The effect of experience on the mating behaviour of the domestic cock. *Anim. Behav.*, **6**, 68-71.

Wood-Gush, D. G. M. (1958b). Genetic and experiential factors affecting the libido of cockerels. *Proc. roy. physiol. Soc., Edin.*, **27**, 6-8.

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DIRECTIONAL DIFFERENCES IN PIGEON HOMING IN SACRAMENTO, CALIFORNIA AND CEDAR RAPIDS, IOWA*

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Kramer, Pratt & St. Paul (1956) reported that the results of pigeon homing investigation at Wilhelmshaven, Germany, and at Durham, N.C. gave superior performance when the pigeons were taken south for release and the worst results when they were taken north.

In a more recent paper Kramer, Pratt & St. Paul (1958) reported further evidence of directional differences in both Western Germany and the South-eastern United States which largely confirmed the pattern reported previously.

Experiences of Sacramento racing pigeon fanciers indicated that homing performance of birds taken south for release was poor as compared with releases from other directions. For this reason, the opportunity which arose to conduct a series of experiments in the Sacramento region was seized, and this was followed up by experiments along similar lines near Cedar Rapids, Iowa. This paper will describe these two series of experiments on directional effects in homing.

The Sacramento Experiments

Description of the Loft and Management of the Birds

The loft housing the birds used in the Sacramento experiments was located about two miles north-east of the city in an area that is flat for several miles in all directions, with very few large trees, and covered with closely-spaced and newly-constructed houses. On exceptionally clear days the mountains north, east, and west of Sacramento can be seen from the loft area. The pigeons were kept in six cubical pens measuring a yard on each dimension and with the bottoms and the sides facing east being of mesh wire.

The birds were forced to fly one hour each morning and evening, and they were kept in the pens the rest of the time. During the exercise flights the birds usually circled a little above the tops of the houses within one fourth of a mile of the loft. On rare instances they would fly out of sight over some pasture land to the south, but they were never gone more than 15 minutes. The first time they were transported away from the loft was on the first experimental release. The ages of the birds at the beginning of the series of releases varied from 3 to 12 months.

Orientation Observed at Release Points North and South of the Loft

Two separate series of releases were made in which the birds were watched through binoculars after release until they were lost from sight. The sun was visible on all releases and the wind was never excessively strong. Thirty-five birds were used at the start of the series of releases on 30th June, 1955. Releases were made in the sequence: 6 miles S, 6N, 10S, 10N, 15S, 15N, 25S, 25N, 50S, and 50N. The birds were released in groups of 5 to 7 birds on the first four releases, then groups of 2 or 3 on the next four and then singly at 50 miles. The vanishing directions of these birds are shown by the solid circles plotted in Fig. 1, only one vanishing point being marked for each sortie regardless of the number of birds involved.

Twenty fresh inexperienced birds were used for a second series of releases from the same release points up to 25 miles. These releases started on 25th July, 1955, at the six mile north point and all birds were released individually throughout this series. The bearings of all birds at the time of vanishing as seen by 20×50 binoculars are shown by the open circles in Fig. 1.

At all distances the vanishing points of the birds released north of the loft were closer to the homeward direction than were those of birds released south of the loft. At 15 miles the difference between N and S is especially pronounced. The birds released to the north at this distance departed very close to the homeward direction

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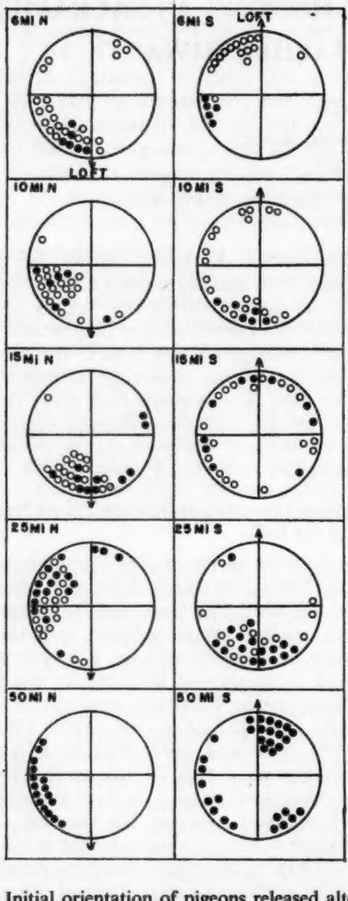


Fig. 1. Initial orientation of pigeons released alternately N and S of the loft. Solid circles indicate first series of releases beginning at 6 miles S on 30th June, 1955, and open circles indicate a second series using a fresh group of birds which began at 6 miles N on 25th July.

while those released to the south scattered in all directions. The birds released at this 15 mile S point also lingered in the vicinity of the release point longer than those released at any other point. The birds released 25 miles south of the loft left the release area quickly but they were concentrated very close to the exact opposite of the homeward direction.

In general the second series of releases gave results which were consistent with the first. However, the 6 mile N, 6S, 10S, 15N, and 25 N releases gave small shifts in the average bearings which could be interpreted as due to day-to-day variations in homing performance such as were reported by Schmidt-Koenig (1958).

Although no exact record was made of homing speeds in these experiments it was apparent from general observation that the birds released to the south were somewhat slower to return to the loft and more birds failed to return from that direction.

Directional Differences in Homing Speeds

In the spring of 1956 experiments were performed to test for directional differences in homing speeds in the Sacramento region. These tests were designed to provide simultaneous releases from the four main directions—the "cross" experiment—along the lines first introduced at Duke University (see Kramer, Pratt & St. Paul, 1956).

Ninety-seven pigeons from 3 to 12 months in age which had experienced only daily exercise flights around the immediate vicinity of the loft were used for these experiments. Eighty of the pigeons were randomly separated into four groups of 20 birds and those remaining were used to replace lost birds in order to keep nearly 20 in each group.

Simultaneous releases were made from points north, east, south and west of the loft at 3·25, 15, and 40 miles. Simultaneous north and south releases were made at 90 miles. Single birds were released at each point at 15 minute intervals on the first two release days and at 10 minute intervals thereafter. Releases were made daily for the 3·25 and 15 mile flights, 3 days elapsed between the 40 mile flights, and 7 days between the 90 mile flights. On successive release days, the direction of displacement of individual birds was shifted. The sequence for the birds that were first displaced to the north was a repetition of the cycle N, S, W, E; the others were rotated in step with these. The first four "cross" releases were made from 3·25 miles allowing each group to fly from each direction, the next four from 15 miles and the last two from 40 miles.

For the 90 mile release the pigeons were reassembled into two groups in such a way that none of the birds to go north had flown from that direction on their last flight and similarly for the group picked to go south. The groups were reversed in direction and flown a second time from 90 miles.

Observers at the loft recorded the time of arrival of each bird. The comparisons of performance are based entirely on the speed of homing. When two or more pigeons arrived at

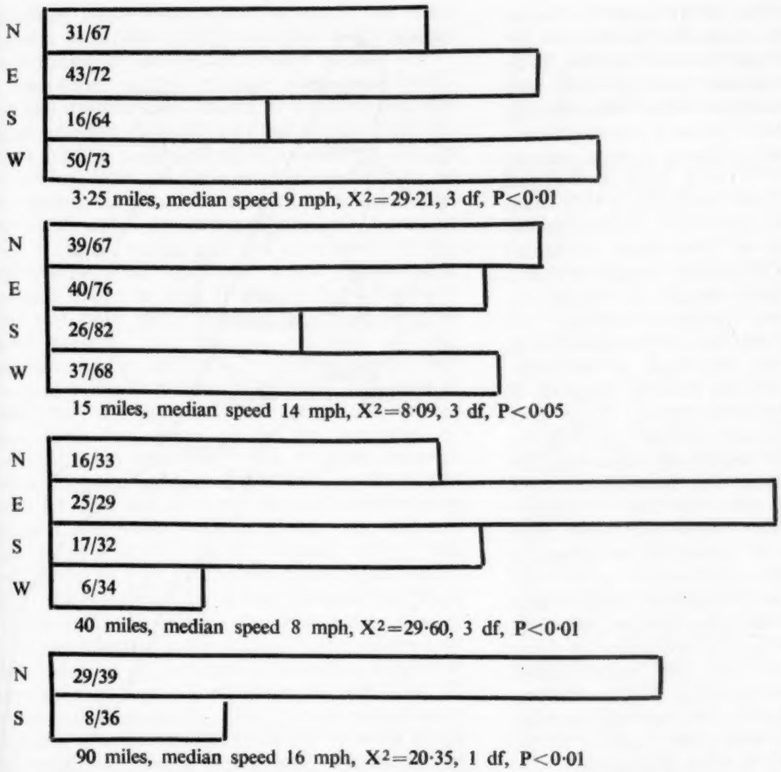


Fig. 2. Percentage difference in homing success of Sacramento pigeons dependent on displacement direction (indicated on left) for 3·25 miles (top), 15 miles, 40 miles, and 90 miles. The fractions within each bar show the numerical results for each direction: the numerator is the number of birds homing equal to or faster than the median speed for the distance; the denominator is the total of the homing speeds observed for that distance.

the loft from the same release point simultaneously, only the speed of the fastest bird was considered in the compilation of results.

Fig. 2 provides a summary of the results. For each distance the approximate median speed was calculated. The horizontal bar graphs show percentages of birds from the four directions making speeds equal to or greater than the median for each distance. The fractions at the left hand side of the graphs show the numerical results for each direction; the numerator is the number of birds equal to or faster than the median; the denominator is the total of the homing speeds observed. The chi-square analysis applied was one testing the similarity among the ratios of "fast" to "slow" birds for the four directions in a 2 × 4 table.

Three of the four distances tested yielded results that showed clearly significant differences in performance among the four directions and the differences at the fourth distance (15 miles) were marginally significant. However, there was a lack of consistency of direction effects: at 3·25 miles, W gave the best performance and S the worst; at 15 miles, N, W, and E were approximately equal and S poor; at 40 miles, E was best and W worst; whereas in the two-direction comparison at 90 miles N was better than S. This variation was greater than that reported previously for other regions studied. A careful analysis of the weather conditions prevailing on the release days indicated that they probably had no significant influence on the directional difference results. A study of possible topographical factors gave promise of explaining at least some of the direction differences. The results are discussed from this point of view in the following section.

The Sacramento Results in Relation to Topographical Factors

Several observers have reported an influence of topography on the flight of homing pigeons. Yeagley (1951) observed that pigeons had to be taught to cross mountain ridges and that they almost invariably detour to fly over towns if they happen to be within a few miles of their course. Griffin (1952) reported a tendency from some birds to follow linear landmarks such as railroads, highways, and the shores of the Finger

Lakes. Hitchcock (1952, 1955) noted that some of his birds showed a decided preference for wooded rather than open country and ridges or minor outcroppings to level land. His birds also avoided crossing a wide lake when released near its shore. At times they followed a contour on a slope rather than maintaining a true course. Pratt & Thouless (1955) and Pratt & Wallraff (1958) have reported that the location of a town near a release point gave rise to false initial orientation for some of their birds. Arnould-Taylor & Malewski (1955) have suggested that a large number of positive results in homing experiments may be due to topographical cues.

After the results of the above experiments were known, a careful study was made of the topography around Sacramento with the purpose of trying to find any possible factors which may have influenced the results. At the 3·25 mile release points different conditions regarding the distribution of residential and uninhabited areas were noticed. The north point had a concentrated residential section to the southwest, with open fields and widely scattered buildings in other directions. The east release point was located in a concentrated residential section with a less heavily populated area toward the east. The south point had about two miles of open country towards the loft and concentrated residential sections to the west and southwest. The west point was located on the western edge of North Sacramento with dense housing to the east and open country in other directions.

Pigeons kept at the Sacramento loft showed a preference for flying over houses rather than open fields. The results for the 3·25 "cross" releases are consistent with the interpretation that birds homed faster when the housing development attracted them in the home direction.

A study of the topography in the vicinity of the 15 mile release point did not suggest any features which might have caused the results obtained. It may be noteworthy that the direction effect, while apparently present, was less striking than at other distances where possible topographical factors were found.

Only two releases were made at 40 miles because the stock of birds available was depleted by heavy losses from the west. The first west release at 40 miles was made about five miles south of the due west line (point A, Fig. 3). Ten of the 15 birds did not get home on the release day, while the east birds made exceptionally good time. On the second 40-mile release the birds to be released west of the loft were split

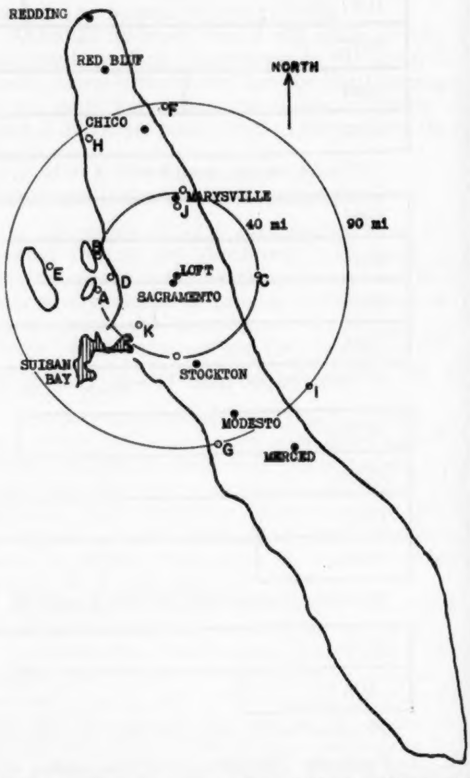


Fig. 3. Outline of some of the California valleys with broad flat floors. Release points from 35 to 90 miles are indicated by open circles and those referred to in the text are labelled with capital letters. Solid circles show location of major cities.

into two groups of ten each. Those of one group were released at the original point, and the others were taken to a spot 40 miles from the loft but five miles north of due west (point B, Fig. 3). The results were bad from both west points, while those from the east remained good. The 40-mile east point was located on the western slopes of the Sierra Mountains at an elevation of 2,400 feet in a dense pine forest (point C, Fig. 3). The Sacramento Valley is plainly visible from this spot. Both of the 40-mile west points were in the western range of mountains. This range is treeless and several valleys with wide flat floors were visible to the west of the release points. It is thus conceivable that the birds released to the west could have been misled by the valleys in the

direction away from home in much the same manner as Griffin (1952) surmised that his birds were fooled by one of the Finger Lakes.

Two other western releases were made (without any simultaneous release at the same distance from another direction) to get further information on the suggested effect of valleys. (1) On 26th May, 1956, 16 birds were released singly on the eastern slopes of the western mountain range about 35 miles due west of the loft (point D, Fig. 3) from a spot where the Sacramento Valley was visible. This was done to test the idea that homing might be poor in general from the west, and not only when misleading valley features were present. The pigeons released on this occasion had no difficulty in reaching home; but in spite of the fact that the distance was only 35 miles they did not attain the speeds the 40-mile east birds had made on the two previous releases. (2) On 23rd July, 1955, 18 birds left over from the heading studies presented at the beginning of this report were released individually from a fire tower on top of Mt. St. Heleana (elevation 4,343 ft.) about 68 miles west of the loft (point E, Fig. 3). The birds were reluctant to leave the release cage and they flew into the Napa Valley in the direction away from home. Out of 22 birds released none reached home on the first day and most of them never did return in spite of the fact that they had all flown recently from 50 miles north and south. Thus it appears that poor homing is quite general from the western range of mountains, and it is not clear whether or not misleading topography is the major inhibiting factor.

Two releases were made at 90 miles. The first release was from points nearly north and south (points F and G, Fig. 3). Homing was good from the north and very poor from the south with only three birds returning from that direction on the first day. The north point was close to the eastern range and the south point close to the western range of mountains.

On the second 90-mile release the north and south groups were both split into two equal parts to test the idea that good homing always occurs from the eastern side of the Central Valley and poor results from the western side. The original points were used again and also two new 90-mile points, one NNW against the western range of mountains (point H, Fig. 3) and the other SSE against the Sierras (point I, Fig. 3). Both north points gave good returns while the results were poor from each of the south positions.

There were mountains close by on three sides of each of the 90 mile north points, with the open side toward home; while the south birds had mountains on only one side. This suggests a possible interpretation in terms of topographical features.

An Experiment to Test the Effects of Topography

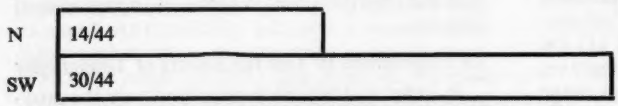
In order to examine more objectively the possible influence of topography on homing success we planned another set of releases. The object was to pick a south location where the topography would be predicted to aid the birds and a north point where it should hinder them. In this manner an attempt would be made to reverse the usual result of poorer homing from the south when compared to the north.

For this purpose we chose a north point 36·5 miles from the loft and just a fraction of a mile south of the city of Marysville (point J, Fig. 3) with the idea that the presence of the city should attract the birds in the wrong direction. The other point was chosen 37 miles southwest of the loft (point K, Fig. 3). There are no cities within 10 miles of this point, and the direct route to Sacramento is free of towns. In addition there are hills and Suisan Bay visible in the opposite direction which was expected to encourage departures toward the loft.

Sixty young racing pigeons, raised from the same breeding stock which produced the birds used in the earlier tests, were used in this experiment. Their management was the same as that of the previous group, and they were 3 to 4 months of age at the beginning of the experiment. To get them accustomed to being handled the birds were "single-tossed" twice from points within two miles of the loft, first from the south and then from the east a week before the main experimental releases. Once again the birds gave evidence at this short distance of their preference for flying over houses and of their reluctance to cross open fields. At both release points they were released with an open field about a quarter of a mile wide between them and the loft, and they flew away from home and circled over the nearby houses a few minutes before coming back to cross the field.

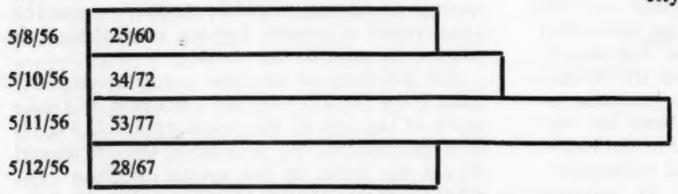
Fifty of the pigeons were then randomly separated into two groups of 25 birds each and the remainder reserved to substitute for those lost on the first release. Simultaneous releases were made from the two 37-mile points. The groups were then reversed for a second release from the same points. Fig. 4 provides a summary

of the results by the method previously described. The results from the south were significantly better than those from the north, as was predicted on the basis of the selected topography.



37 miles, median speed 8·5 mph, $X^2=11{\cdot}64$, 1 df, $P<0{\cdot}01$

Fig. 4. Percentage differences in homing success dependent on displacement direction for 37 miles. Fractions interpreted as in figure 2. The experimenter successfully predicted that the release points (not previously used) would reverse the earlier N-S results.



3·25 miles, median speed 9 mph, $X^2=14{\cdot}57$, 3 df, $P<0{\cdot}01$

Fig. 5. Percentage differences in homing success dependent on release day (indicated by date on left). The fractions within each bar show the numerical results for each date: the numerator is the number of birds homing equal to or faster than the median speed for all 3·25 mile releases; the denominator is the total of the homing speeds observed for that day.

The weather on the release days provided no explanation of the faster homing from the south.

An Example of Day to Day Differences in Homing Performance

Kramer (1957) has referred to the possibility of daily fluctuations in conditions interfering with homing results. A striking example of this phenomenon occurred during the sequence of 3·25-mile cross releases presented above. Fig. 5 shows the percentage of birds on each day of the 3·25-mile releases which made the median speed for all four days or better. The third release day was far superior to the other three and the speeds from all four directions were improved on this day. The speeds from the best direction improved by a greater amount than the speeds from the worst direction. The performance on the fourth release was poorer than that of the third day. These two days had identical weather conditions. While it is reasonable to suppose that flying experience and the learning of landmarks contributed to the improvement over the first three days, it is not possible to explain at this time the significant decline in performance from the third to the fourth day, except to say that unknown conditions on the fourth day caused poor performance. Apparently exceptional days for homing do occur, they can be observed at only 3·25 miles from any direction, and they cannot be explained in terms of surface weather conditions usually recorded.

The Cedar Rapids, Iowa, Experiments

In the summers of 1957 and 1958 experiments similar to those described above for the Sacramento area were carried out in Cedar Rapids, Iowa. The Cedar Rapids loft was located about a mile east of the Cedar Rapids city limits and a mile south of the city of Marion. The loft was built on top of a hill surrounded by wooded rolling country which contains widely scattered houses. The experimental procedure differed from those presented above only in the fact that the birds were housed in a larger, conventional-type pigeon loft and were allowed to have continuous freedom. In their exercise flights about the loft the birds seemed to prefer to fly mostly over the area to the southeast which was wooded rolling country containing no houses.

Simultaneous releases were made from four points north, east, south, and west of the loft at exactly 3, 15 and 50 miles. Simultaneous east and west releases were made at 110 miles. Two releases were made at 3 miles, three at 15 miles, two at 50 miles, and two at 110 miles.

Fig. 6 provides a summary of the results. For each distance the median speed was calculated and the percentage of birds from each direction making greater than or equal to the median is shown.

The releases at 3, 15, and 50 miles gave similar results, all being characterised by the fact that the birds released to the west were inferior in homing speed to a statistically significant degree when compared with the performance of birds released in the other three directions. The differences between the north, east, and south birds were not consistent from day to day although in the final compilation of results the east birds appear to be slightly superior. A careful analysis of the weather and local topography indicates that it is highly improbable that the results obtained from 3, 15, and 50 miles are in any way dependent upon these factors.

The releases at 110 miles east and west were

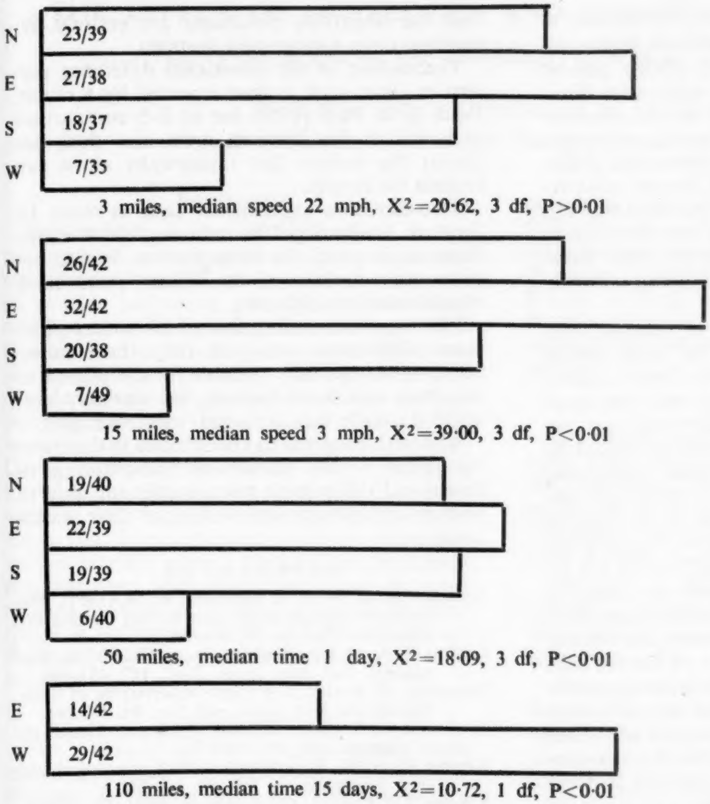


Fig. 6. Percentage difference in homing success of Cedar Rapids pigeons dependent on displacement direction (indicated on left) for 3 miles (top), 15 miles, and 110 miles. Fractions interpreted as in Fig. 2.

made on 19th July, 1958, and 4th August, 1958. On the 19th July overcast skies and very light continuous rain moved from W to E to cover the entire region between the release points. This weather was at the W release point from the beginning of the releases but did not reach the E release point until nearly all birds had been released. The wind was light and variable in the morning becoming E 12-15 knots in the afternoon. Visibility was limited to 4-12 miles.

On the 4th August the weather was clear with good visibility, and light variable winds becoming S at 10-15 knots in the afternoon. However, a small thunderstorm moved toward the E release point from the NW and could have had some effect on the birds released from the E.

The 19th July headings of the birds released to the west were concentrated to the SW and the east birds headed generally to the southeast. On the 4th August the headings of both east and west birds were more scattered even though the sun was more clearly visible than it was on the 19th July. The majority of the west birds still vanished to the SW but the east birds' headings were scattered all around the compass.

Only three west birds homed the first day on the 19th July release and none from the east. Five west birds and one east bird homed on the 4th August release day. Only half the birds had returned by 15 days after the releases. Thus it is clear that even though the west birds were superior in performance when compared to the east birds neither group homed very well (even on the fair weather day). Therefore it seems reasonable to believe that the factors which caused poor performance from the west at the shorter distances may still exist at 110 miles and it is only because the east birds have now been subjected to some new factors which is even more effective that enables the west birds to become superior in the 100-mile E-W comparison. Considering the fact that pigeons cross bodies of water reluctantly it is suggested that this new factor could be the Mississippi river.

Discussion

In releasing pigeons simultaneously from the same distance but different directions from their loft it has been observed that the phenomenon of directional difference in homing speed occurs at widely separated locations and at distances ranging from 3 to 125 miles. The particular pattern of difference has been shown to vary with both the location of the loft and the distance of the releases. There is some indication of day to

day fluctuation in the patterns of difference at least among the best and intermediate directions.

Kramer, Pratt & St. Paul (1958) present evidence that overcast weather reduces the directional difference by reducing speeds from all directions and speeds from the best direction by a larger amount with the same directional difference pattern persisting. The 3·25-mile cross releases in Sacramento gave an indication of this blunting of the speeds from the best direction by a larger amount as compared to the other directions on a clear day in which homing performance in general was reduced.

A 10-mile N-S comparison of pigeons from the same stock that produced the birds used in the Sacramento experiments with Duke University stock was made in Durham with the result indicating that directional differences are not related to genetic factors. Pigeons produced by feral pigeon stock gave the same directional difference pattern from 3 to 15 miles east and west in the Cedar Rapids area as the homing pigeon stock although the losses were quite large.

To what extent directional differences are influenced by topographic factors is not clear. If, as many observers have reported (see page 203), pigeons do detour to fly over towns and around bodies of water, or follow ridges or forests, then this would certainly affect their homing speeds. It is difficult to evaluate from the pigeon's point of view the topographic features over which the birds must fly. A direct test using the same release points but with physiographical features reversed is obviously impossible.

Although it is reasonable to assume topography may influence directional differences to some extent, there are observations which point strongly toward unknown factors which also influence the results. Whenever it has been possible to observe the headings of pigeons, those released in the poor direction show orientation difficulties at the release point by either heading in the wrong direction or scattering at random after lingering in the area longer than usual, while those released in the best direction usually fly off quickly and vanish close to the home direction. The work of Schmidt-Koenig (1958), which shows that headings even at short distances can be altered by shifting for a few days before release the light-dark cycle under which the birds live, makes it unreasonable to believe that the departure directions are entirely dependent upon topographic features.

Fluctuation of the directional difference pattern in time, such as that reported by Kramer, Pratt & St. Paul (1958) for an E-S comparison at a loft in the Durham area, also does not favour the notion that topography alone can explain the results.

Two-direction experiments such as those by Pratt & Wallraff (1958) indicate that it is the direction in which the birds have to fly and not some characteristic of the release point itself which causes the difficulty.

The most astounding fact of all is that significant differences occur at only three miles. Surely it is physically possible for the pigeon to see, from this short distance, the territory over which it usually flies in its daily exercise flights.

Although progress has been made in discovering some of the conditions contributing to directional differences, we are still not able to provide a complete explanation of their occurrence.

REFERENCES

Arnould-Taylor, W. E. & Malewski, A. M. (1955). The factor of topographical cues in bird homing experiments. *Ecology*, **36**, 641-646.

Griffin, D. R. (1952). Airplane observations of homing pigeons. *Bull. Mus. comp. Zool.*, **107**, 411-440.

Hitchcock, H. B. (1952). Airplane observations of homing pigeons. *Proc. Amer. phil. Soc.*, **96**, 270-289.

Hitchcock, H. B. (1955). Homing flights and orientation of pigeons. *Auk.*, **72**, 355-373.

Kramer, G. (1957). Experiments on bird orientation and their interpretation. *Ibis*, **99**, 196-227.

Kramer, G., Pratt, J. G. & Von St. Paul, U., (1956). Directional differences in pigeon homing. *Science*, **123**, 329-330.

Kramer, G., Pratt, J. G. & Von St. Paul, U. (1958). Neue Untersuchungen über den "Richtungseffekt". *J. Orn.*, **99**, 178-191.

Pratt, J. G. & Thouless, R. H. (1955). Homing orientation in pigeons in relation to opportunity to observe the sun before release. *J. exp. Biol.*, **32**, 140-157.

Pratt, J. G. & Wallraff, H. G. (1958). Zwei-Richtungs-Versuche mit Brieftauben. *Z. Tierpsychol.*, **15**, 332-339.

Schmidt-Koenig, Klaus (1958). Experimentelle Einflussnahm auf die 24-Stunden-Perodik bei Brieftauben und deren Auswirkungen unter besonderer Berucksichtigung des Heimfindevermögens. *Z. Tierpsychol.*, **15**, 301-331.

Yeagley, H. L. (1951). A preliminary study of a physical basis of bird navigation. Part II. *J. appl. Phys.*, **22**, 746-760.

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THE EFFECT OF OESTROGEN AND PROGESTERONE ON THE NEST-BUILDING OF DOMESTICATED CANARIES

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Introduction

Nest-building in female birds occurs during the seasonal recrudescence of the gonads and reproductive tract. This suggests that it depends on ovarian hormones, but there is little direct evidence about the precise ones involved. Until recently studies involving oestrogen treatment of non-breeding females had demonstrated morphological changes, but no effects on nest-building had been reported. Lehrman (1958), however, noticed building behaviour in Ring Doves (*Streptopelia risoria*) after oestrogen treatment. It seemed, therefore, that the earlier negative results in other species could have been due to insufficient dosages or periods of administration. Further, since a combination of exogenous oestrogen and progesterone may be more efficient in inducing oviduct growth in chickens (Brant & Nalbandov, 1956) and doves (Lehrman & Brody, 1957), it may also be effective for nest-building.

Procedure

The canaries, of the Border variety, were paired and placed in metal cages (described in Dunnett & Hinde, 1957) and supplied with a standard plastic canary nest-pan. The experiments were started in October, after the moult, and at intervals thereafter through November, December and January.

Each pair was watched on at least seven days before the first hormone injection, and usually daily for at least two weeks afterwards. Building material—grass and feathers in small wire-netting baskets—was supplied for the duration of each watch; all material was then removed. Each watch lasted 12 minutes, and detailed records of building behaviour were taken as described previously (Hinde & Warren, 1959); in particular, the number of times each bird carried material, and the number of times it placed material in the nest-pan were recorded.

The injections were given in the pectoral musculature three times weekly. Hormones used were aqueous suspensions of oestradiol benzoate (Oestroform Aqueous B.D.H.) and progesterone (Lutoform, B.D.H.). The dosages of oestradiol were 0·1—0·15 mg. (1 mg./ml.); 0·25—0·3 mg. (2 mg./ml.) and 0·5 mg. (5 mg./ml.). The dosage of progesterone was 0·125 mg. (5 mg./ml.). Control animals were injected with 0·1 ml. of Frog Ringer solution. A total of 76 females and 6 males were injected; they were distributed between groups as shown in the next section.

Results

The results are shown in Tables I and II. Ten birds which died within the first 10 days after the injections started, and 5 birds which were never seen to carry material, are not included in the tables. The remaining birds in each group were divided as follows:

Category 0. Birds which were seen to carry material, but not to place it in the nest-pan. For these, the mean number of carrying bouts per watch are given.

Category +. Birds which were seen to place material in the nest-pan. For these, the mean numbers of carrying bouts and of placings per watch are given.

(i) *Controls*. (Table I). Seven females, after 7 daily pre-injection tests, were given 0·1 ml. Frog Ringer solution 3 times per week. In two cases the injections were continued for three weeks, and in the other five for over four weeks. These control birds were started at intervals throughout the period in which the hormone experiments were conducted. No control bird was seen to place material, and carrying was rare.

(ii) 0·1—0·15 *mg. oestrogen*. (9 females, Table I). This dose level produced a small but definite increase in carrying but had no definite effect on placing.

Of 4 birds which did not place throughout the experiment, 2 were seen to carry before the injections and all 4 afterwards. The maximum number of carryings in any test after injection was 6. Two of these birds were injected for a fortnight, and two for three weeks.

Of 5 birds which were seen to place, 4 were seen to carry, and 1 to place, before the injections, and all placed after the injections. Thus

Table I. Mean Number of Carrying (C) and Placing (P1) Bouts per Watch Shown by Birds Injected with Oestrogens.

Sex	Treatment	Placed (+) or carried only (0)	No. of birds	Bouts of carrying (C) or placing (P1)	Day w.r.t. 1st injection								
					—7/—6	—5/—4	—3/—2	—1/0	1/2	3/4	5/6	7/8	15
♀	Control Frog Ringer	0	7[1]	C	0·07	0·07	0·28	0	0·16	0·22	0·08	0	0
	0·1—0·15 mg. oestrogen	0	4[2]	C	0	0·6	0·28	0·37	2·3	2·0	2·0	2·4	1·5
		+	5[3]	C	(0)	(0)	0·5	0·87	1·0	(0·25)	1·4	(1·0)	2·2
				P1	(0)	(0)	0·1	0·25	0·25	(0·25)	0	(0)	0·2
	0·25—0·3 mg. oestrogen	0	2[4]	C	0	0	0	0	(1)	0·5	0·5	1·0	1·5
		+	5[5]	C	0	0	0·2	0·3	0·8	1·4	0	1·8	2·8
				P1	0	0	0	0	0	0	0	0·7	2·2
	0·5 mg. oestrogen	0	5[6]	C	0	0	0	0·2	1·4	1·6	1·1	—	—
		+	17[7]	C	0·23	0·53	0·72	0·91	1·7	3·6	2·7	2·7	2·0
				P1	0	0	0·02	0	0·8	2·0	2·1	2·5	2·0
♂	0·5 mg. oestrogen	0	4[8]	C	1·0	1·5	0	0·4	1·0	0·2	0·2	0	—
		+	2[9]	C	0	0	0	0	0	0·5	2·5	3·8	—
				P1	0	0	0	0	0	0	0·75	2·0	

1. Each figure based on 9—14 watches
2. „ „ „ 5—8 „
3. „ „ „ 8—9 „ except figs. in parenthesis, based on 4 watches.
4. „ „ „ 2—4 „
5. „ „ „ 5—10 „
6. „ „ „ 6—10 „
7. „ „ „ 22—36 „ except for days 5—8 (15—19 watches)
8. „ „ „ 4—8 „
9. „ „ „ 2—4 „

the pre-injection performance of these birds was better than that of the 4 birds which never placed. The maximum number of carrying bouts per test was 7, and of placings 1.

(iii) 0·25—0·3 *mg. oestrogen.* (7 females, Table I). On average, the effect of this dose level was little greater than that of the previous one, but one bird built vigorously after treatment.

Two birds did not place throughout the experiment; these did not carry before injection but did after. Five birds were seen to place: 3 of these did not carry before injection, but all did afterwards. None of these birds was seen to place until a week after the first injection; after a fortnight, the mean number of placings was 2·2, but one bird carried 9 times and placed 7 times on Day +15, and carried 14 times and placed 14 times on Day 19.

(iv) 0·5 *mg. oestrogen.* (37 females, Table I). Although this dose level was toxic to some individuals, it induced vigorous building in others.

Ten birds died during the first 10 days after injections started. Five others were never seen to carry, and are not included in Table I. Five birds carried but did not place; 4 of these did not carry before injections but all carried after, the maximum number of carrying bouts in any test being 9. Of 17 birds which were seen to place, 14 carried and 1 placed before the injections. Thus the pre-injection performance was better than that of the birds which did not place after injection. There was a marked increase in

Table II. Mean Number of Carrying (C) or Placing (Pl) Bouts per Watch Shown by Birds Injected with Oestrogen and Progesterone (or Progesterone only) after Oestrogen Treatment.

Treatment	Pre-treatment	Placed (+) or carried only (0)	No. of birds	Bouts of carrying (C) or placing (Pl)	Day w.r.t. start of treatment									
					—7/—6	—5/—4	—3/—2	—1/0	1/2	3/4	5/6	7/8	9/10	15/16
0·15 mg. oestrogen and 0·125 mg. progesterone	0·15 mg. oestrogen	0	3[1]	C	2·5	1·4	0·5	1·5	1·2	0	0·8	0·8	—	0
		+	2[1]	C	0·5	1·0	1·5	1·7	2·5	3·3	0·5	2·3	—	2·0
				Pl	0	0	0·3	0	0	0	0	0·7	—	0
0·5 mg. oestrogen and 0·125 mg. progesterone	0·5 mg. oestrogen for 1 wk.	+	4[2]	C	—	0·7	2·2	3·5	3·5	—	3·1	6·3	7·1	9·0
				Pl	—	0	1·5	3·0	3·3	—	2·6	4·8	6·5	9·0
	0·5 mg. oestrogen for 18+days	+	2[3]	C	—	7·5	5·5	6·7	9·0	(1·5)	7·3	5·5	10·0	—
				Pl	—	7·5	5·5	6·3	8·0	(1·5)	7·0	5·5	10·0	—
0·125 mg. progesterone only	0·5 mg. oestrogen +0·125 mg. progesterone	+	5[4]	C	3·9	5·6	7·6	5·9	3·4	0·9	1·2	0·04	—	—
				Pl	3·7	4·6	7·0	4·6	3·0	0·02	0·3	0	—	—

1. Each figure based on 2—5 watches
2. ,, ,, ,, 4—8 ,,
3. ,, ,, ,, 2—4 ,,
4. ,, ,, ,, 5—10 ,,

building behaviour after the injections started, and all 17 birds placed; the maximum number of carrying bouts and placings was 15.

(v) 0·15 *mg. oestrogen* + 0·125 *mg. progesterone*. (Table II). The addition of progesterone to low levels of oestrogen produced no definite effect on nest-building.

Five females were treated with 0·15 mg. oestrogen thrice weekly for 3 weeks or longer, and then given 0·15 mg. oestrogen + 0·125 mg. progesterone thrice weekly. Three of these birds did not place either with oestrogen alone, or with oestrogen and progesterone. Two birds were seen to place both before and after the oestrogen and progesterone injections: there was no clear evidence that the slightly higher mean number of carrying bouts with progesterone was due to this hormone. Taking all five birds together, there was no increase in carrying after progesterone treatment.

(vi) 0·5 *mg. oestrogen* + 0·125 *mg. progesterone*. (Table II). The addition of progesterone to high levels of oestrogen also produced no definite effect.

Six females were treated with 0·5 mg. oestrogen + 0·125 mg. progesterone after previous oestrogen treatment. Four of these had had one week's pre-treatment with oestrogen, the other 2 had been on oestrogen for 18 days and 40 days respectively. All 6 placed while on oestrogen alone. The 4 birds which had one week's pre-treatment with oestrogen showed a gradual increase in building behaviour during the period on oestrogen, but no marked further increase during the first week on progesterone. They did show a high mean number of carryings and placings after this point, but similar scores were obtained with birds which were kept on 0·5 mg. oestrogen alone for the same period (see, for example, the pre-progesterone period of the 2 birds which had been on oestrogen for 18+ days). The 2 birds which had a prolonged pre-treatment on oestrogen also provided no clear evidence that progesterone either increased or inhibited building.

(vii) 0·125 *mg. progesterone only*. (Table II). Progesterone alone did not maintain the building behaviour previously induced by oestrogen

Five females were treated with oestrogen and progesterone as in (vi) and then given 0·125 mg. progesterone only thrice weekly. All these were placing on oestrogen + progesterone; the building behaviour fell off rapidly when the oestrogen was stopped. There was no placing on or after Day +6.

(viii) *Males treated with* 0·5 *mg. oestrogen.* (6 males, Table I). High doses of oestrogen caused an increase in building in some males.

Six males were given 0·5 mg. oestrogen thrice weekly. Four did not place throughout the experiment, and showed no increase in the frequency of carrying as a result of the treatment. Two others did not carry or place before the injections, but began to do so 6 days after the injections started.

Survival

Although injections of 0·5 mg. oestrogen were effective in inducing nest-building, they also had a toxic effect on some individuals. Of 37 birds injected, 10 died in the first 10 days after injections started, and others later. None of the control animals, and none of those injected with 0·1—0·15 mg. or with 0·25—0·3 mg. died in the three weeks after injections started. Thus the margin between the effective dose and the lethal dose is rather small.

Discussion

The results presented above indicate that large doses of oestrogen can induce nest-building behaviour in canaries during the non-breeding season. Progesterone alone, in the dosage used, does not. The building behaviour of many of the females treated with 0·5 mg. oestrogen included all the building movements used in nest construction and was at least qualitatively similar to that shown in the natural breeding season. Although there was no precise correlation between pre-and post-injection behaviour, the hormone was usually more effective in birds which had shown some building before treatment.

Little previous work on the effects of oestrogens on avian behaviour has been reported. They are known to induce sexual responses in domestic fowl (reviews in Beach, 1947; Collias, 1950), but Emlen & Lorenz (1942) found no indications of sexual behaviour in Valley Quail (*Lophartyx californica*) after implants of stilboestrol pellets, and Noble & Wurm (1940) claimed that, in the Black-crowned Night Heron (*Nycticorax nycticorax*), "no phase of the female behaviour is due to oestrogens." Shoemaker (1939) used oestrone on female canaries, and did not observe any effect on behaviour. Sexual behaviour was not studied in the present experiment, but it is usually associated with nest-building and it is likely that both are influenced by the same hormones. There are thus some apparent discrepancies in the evidence—oestrogens induce sexual behaviour in hens but appear not to do so in Quail or Herons, and the effect on the nest-building of canaries in this paper is not paralleled in the other studies. These may be considered as follows:

(*a*) *The behaviour studied.* The authors cited above were concerned primarily with female sexual behaviour. This is influenced by the previous behaviour of the male, and thus any failure to detect an effect of oestrogens on sexual behaviour could be due to a deficiency in the males. Nest-building can be elicited reliably from canaries in the appropriate conditions, but functionally comparable behaviour in Quail and domestic hens is relatively inconspicuous.

(*b*) *Dose levels.* The dosages effective in the present study were high, and near the lethal level. Low dosages were relatively ineffective. We have no means of knowing whether the amount of oestrogen injected is greater than that normally secreted by the ovary, but the hormones used were synthetic products manufactured for use in mammals, and there may be chemical differences between avian and mammalian oestrogens. It is also possible that, during the off-season, there is a refractoriness of the sensory-neuromuscular mechanisms to oestrogens comparable to the suggested refractoriness of the pituitary and gonads (e.g. Marshall, 1954).

(*c*) *Species differences.* Some of the apparent discrepancies could be due to differences in the species used. However, the results of this study indicate that if the dose level is high enough, oestrogens do influence reproductive behaviour in canaries.

Since the smaller doses of oestrogen had only a limited effect on nest-building, and the larger doses were toxic to some individuals, combinations of oestrogen and progesterone were tried. Although oestrogen tends to inhibit some aspects of parental behaviour in mammals, it induces mammalian oestrous more predictably when given in combination with progesterone (e.g. Boling *et al.*, 1938; Ring, 1944). Further, although birds have no corpus luteum, progesterone has been demonstrated in the blood of

hens (Fraps, Hooker & Forbes, 1948); and Lehrman (1958) has shown that the oviducts of Ring Doves enlarge more when oestrogen is given in combination with progesterone than when it is administered alone.

In the doses used in this experiment, progesterone did not produce any appreciable augmentation of the action of oestrogen—nor, on the other hand, did it suppress it. It is known, however, that the effects of oestrogen and progesterone on reproductive morphology depend on the relative as well as the absolute amounts of each; and indeed opposite effects may be induced by varying the dosage (Mason, 1952). It is therefore still possible that progesterone would be found to play a role in other dosage combinations.

Summary

1. Female canaries were injected with various levels of oestrogen and of oestrogen in combination with progesterone.

2. Doses of oestrogen from 0·1 to 0·3 mg. thrice weekly had a negligible effect on building behaviour. Doses of 0·5 mg. thrice weekly were toxic to some individuals, but produced active nest-building in others.

3. No enhancement or inhibition of the effect of oestrogen by progesterone was found in the dose combinations used. Progesterone alone did not maintain building behaviour previously induced by oestrogen.

4. Doses of 0·5 mg. oestrogen induced nest-building in some males.

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REFERENCES

Beach, F. A. (1947). *Hormones and behaviour*. New York: Hoeber.

Boling, J. L., Young, W. C. & Dempsey, E. W. (1938). Miscellaneous experiments on the oestrogen-progesterone induction of heat in the spayed guinea pig. *Endocrinology*, **2,** 182-87.

Brant, J. W. A. & Nalbandov, A. V. (1956). Role of sex hormone in albumen secretion by the oviduct of chickens. *Poult. Sci.*, **35,** 692-700.

Collias, N. E. (1950). *Hormones and behaviour, with special reference to birds and the mechanisms of hormone action.* In Symposium on Steroid Hormones, Ed. E. S. Gordon, Univ. of Wisconsion.

Dunnett, G. E. & Hinde, R. A. (1957). Chapter on Canaries in *U.F.A.W. Handbook of Laboratory Animals*. London: U.F.A.W.

Emlen, J. T. & Lorenz, F. W. (1942). Pairing responses of free-living Valley Quail to sex hormone implants. *Auk*, **59,** 369-376.

Fraps, R. M., Hooker, C. W. & Forbes, T. L. (1948). Progesterone in blood plasma of the ovulating hen. *Science*, **108,** 86-87.

Hinde, R. A. & Warren, Roslyn P. (1959). The effect of nest-building on later reproductive behaviour in the domesticated canary. *Anim. Behav.*, **7,** 35-41.

Lehrman, D. S. (1958). Effect of female sex hormone on incubation behaviour in the ring dove (*Streptopelia risoria*). *J. comp. physiol. Psychol.*, **51,** 142-145.

Lehrman, D. S. & Brody, P. (1957). Oviduct response to estrogen and progesterone in the Ring Dove. (*Streptopelia risoria*). *Proc. Soc. exp. Biol.* (N.Y.), **95,** 373-375).

Mason, R. C. (1952). Synergistic and antagonistic effects of progesterone in combination with estrogens on oviduct weight. *Endocrinology*, **51,** 570-572.

Marshall, A. J. (1954). *Bower Birds*. London: Oxford University Press.

Noble, G. K. & Wurm, M. (1940). The effect of testosterone propionate on the Black-Crowned Night Heron. *Endocrinology*, **26,** 837-850.

Ring, G. R. (1944). The estrogen-progesterone induction of sexual receptivity in the spayed female mouse. *Endocrinology*, **34,** 269-75.

Shoemaker, H. H. (1939). Effect of testosterone propionate on behaviour of female canary. *Proc. Soc. exp. Biol.* (N.Y.), **41,** 299-302.

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TERRITORIAL RANK IN STARLINGS

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Although the problems of territorialism and of social rank have been observed and discussed for many years, the relation of the two behaviour phenomena to each other is by no means clear. In some taxonomic groups territorial behaviour occurs while in other groups social rank behaviour occurs. The occurrence of both types of behaviour has been reported for captive doves (Bennett, 1942), some fish (Fabricius, 1954) and mice (Crowcroft, 1955; Davis, 1958). The research here reported describes the relation of territory to rank in wild and captive starlings (*Sturnus vulgaris*). In addition some other aspects of behaviour are mentioned.

The behavioural studies have been conducted for several years in Baltimore, Maryland, where large numbers of starlings breed. The local, non-migratory birds are augmented in winter by migrants from the north. The birds nest in natural cavities and readily occupy nest boxes, which can be placed in locations suitable for research. The conventional procedures for observation with binoculars were used. The observations were described on a tape in the field and then transcribed and summarized. The observations of captive birds were made in a room about 12 ft. × 14 ft. that contained various numbers of males and females. Food (canned dog food mixed with chicken mash) and water were available at one place. The birds were watched through a one-way mirror and reported on a tape recorder.

These conventional methods have some deficiencies. The first is the chronic problem that many hours are required and therefore only a few individuals may be observed. Some 600 hours were spent in observation of three boxes from October to June, 1956-58 in addition to miscellaneous observations in other years. Unfortunately this paper, like most behaviour papers, has only limited generality because so few individuals can be observed.

The other deficiency is that few wild starlings were individually marked. Unfortunately both male and female starlings destroy the eggs if captured on the nest either in day or night. The male may maintain possession of the box but the females desert. Marking is further prevented by our inability to catch local birds in traps or nets except occasionally when snow covers the ground (migrants are readily trapped). From October, 1957, to May, 1958, birds that entered nest boxes were caught even though it was expected that each would desert that box. During this time (Table I) 5 adult males, 5 subadult males, 6 adult females and 4 subadult females were banded with colours. Although all deserted the box many remained in the area and used another box or hole later. Some males were never trapped because in the fall they rarely enter the box after their first few days of exploration.

Table I. Sex and Age Composition of Starlings Captured at Boxes October, 1957, to June, 1958. (This sample is not random in respect to composition or to time). Age characters described in Davis, 1959).

Month	Males		Females	
1957	Adult	Sub-adult	Adult	Sub-adult
October	1	1	0	0
November	1	1	1	1
December	0	1	0	0
March	3	0	3	1
April	0	2	2	2
	5	5	6	4

Most of the observations were obtained in a suburban area where large oaks, tulip trees, and maples provide a "forest" canopy 150 feet high. The understory consisted of the usual flowering trees and shrubs of residential districts. The starlings fed regularly on the lawns or flew to nearby open areas. Three boxes were used. The locations were changed partly for experimental reasons and partly because a tree blew down. The details of locations are unimportant.

For orientation of the reader a general description of the annual cycle is helpful. During July and August the birds moult and are reproductively inactive. By October most males have obtained nest holes which they defend. The females also defend holes but the fighting is not

vigorous and hence is inconspicuous. Defence of the holes becomes less active in winter but by February becomes more active. Copulation occurs in early April and eggs are laid in late April. Additional broods may be had even in July. Details of the behaviour will be discussed below. The relation of behaviour to the male reproductive organs has been elaborated (Hilton, 1958).

Vocabulary

A knowledge of the functions of the calls of a species is essential for understanding behaviour. Although the function of some notes has not been determined, some notes have clear functions and can be described. As is the custom, names for the notes are provided that are helpful, at least to the author, in discussion of function.

1. *Masculine Aggressive:* (*a*) *Crowing*. The commonest note is a rasping chuckle, repeated monotonously from a perch. Usually the feathers of the lower throat are extended with each note so that a rhythmic sound and motion occurs. The volume varies according to circumstances. The bill is usually pointed upward at an angle during the crowing. The crowing is used by caged birds to establish dominance and to defend a nest box in the room. Crowing is clearly an aggressive note used to attack or repel. A common behaviour sequence is as follows: a new male arrives at a hole; the owner flies to the stranger, perches beside him and begins to crow and puff the throat feathers; the stranger may leave or may begin crowing and puffing; usually the owner, while crowing, will nudge the stranger and push him away along the branch or wire; the crowing by both birds may become very loud.

(*b*) *Scream*. A very loud, high-pitched note is given by a male when birds approach from a distance. It is usually accompanied by vigorous wing-waving. It appears to be aggressive.

2. *Attract female:* (*a*) "*Killdeer*". This call is named for its obvious resemblance to the call of *Charadrius vociferus*. Starlings give the "killdeer" call as early as November and continue all winter. Its function appears to be a long distance notification to a female that the male owns a nest hole. (*b*) *Crescendo*. Another note is a high-pitched ascending and descending phrase used in March and April. It appears to be an urgent notification of availability. (*c*) "*Whew*". An additional note is a soft call, given by the male when he is showing his hole to the female.

3. *Personal song*. A large number of songs or phrases of other species are imitated by starlings and here are called personal because each bird seems to have its own. Several birds, banded with colours, had personal songs. One bird that owned a box for spring of 1957 imitated the alarm of a redwing (*Agelaius phoenecius*). Another bird arrived on 26th March, 1958 and was banded the next day. It regularly gave a call that resembled the call of the red-bellied woodpecker (*Centurus borealis*). Another bird owned a hole in a big oak for a week and regularly imitated the gurgle of a cowbird (*Molothrus ater*) Another bird imitated catbird (*Dumetella carolinensis*), robin (*Turdus migratorius*) and blue jay (*Cyanocitta cristata*) notes. One bird (whose history is described in detail below) had a characteristic "warble" that did not mimic any recognisable song. This warble was used in direct reference to a female several times. For example, once this male showed a female the box by the "whew" call and the female entered the box. The trap-door was pulled shut and he continued to warble even though the female was invisable.

4. *Feminine aggressive*. A "rattle" is given by a female when she attacks another female at a nest site. This note also occurs at the roost at night and may be the feminine version of crowing.

5. *Alarm notes*. Both sexes give a harsh "chuck" which clearly means that a crow, cat, man, or other danger is present. In addition a "rasp" is given when a person or crow is disturbing the nest. The "rasp" is used in the fall as well as the spring.

6. *Flocking call*. A raucous grating call is given by adults and juveniles when they form the post-breeding flock. The note may be given by a single bird as it flies to join the flock.

7. An assortment of whistles, chuckles, and other notes are produced but their functions, if different from those above, have not been determined. The female has a soft "chuck" call whose function is not clear. Its use may be to show the nest site to the male.

Parenthetically it should be noted that the male has "long-distance" and "short-distance" means of communication. The "scream" warns birds while still at a distance and the "crowing" serves for near birds. The "killdeer" call attracts the female from a distance and the "whew" call points out the nest hole to a nearby female.

Aggressive Behaviour

The captive birds in a room arrange themselves in a definite social rank (Davis, 1957) that is essentially the same as the type found in Domestic Fowl and many other species. Table II shows the results of encounters in a group of two males and two females. The rank is clear and was stable from 19th February to 22nd March, 1957. Note that the males dominated the females in this group. Many other groups, castrate males as well as in normals, showed rank clearly. Away from the feeding tray the birds crow and puff their throat feathers. The typical behaviour in captivity is as follows: a bird perches on a pipe, while others are feeding or drinking; another bird flies up to the pipe, perches, and begins to crow and to puff the throat feathers; if the first bird responds by puffing then the second increases its activity and both may crow and puff the throat feathers; eventually one quits and leaves and the other remains, often preening; if the first bird does not respond, it usually promptly moves away at least a few inches. Females show essentially the same behaviour but at a much lower intensity. This behaviour occurs in a room in the absence of nest boxes.

Table II. Example of Social Rank of Starlings. Results of Fights During February and March, 1957, in Captivity

			LOSER			
			Male		Female	
			G	R	W	Y
WINNER	Male	G	–	12	17	8
	Male	R	1	–	8	1
	Female	W	0	1	–	5
	Female	Y	0	0	2	–

Exactly the same behaviour occurs in the wild birds. Usually the conflicts occur between a stranger and the owner of a nest hole. The owner regularly perches between the stranger and the hole and by short hops along the perch forces the stranger away. In one case an owner gradually forced a stranger to move 50 feet along a wire. Generally the owner easily repels the stranger but sometimes actual bodily contact occurs. In prolonged and severe conflicts a curious flipping of the wings occurs. It is a very quick upward motion of both wings. The forearm comes forward and the bird bends the head downwards slightly. It has been performed by both the attacker and defender.

A behaviour called "wing-waving" consists of rapid upward flapping of the wings, while the bird crouches somewhat on its perch. The function of this behaviour is not completely clear. Certainly it is done most vigorously in the month before laying but it may be done weakly ("half wing-wave") in September or October. It is most characteristically given with the "scream" call and clearly serves as a visual warning to a bird that is flying over. However it may also be given with the "Killdeer" call at a female. Perhaps it serves the double advertising function to male and female alike that "here is a male that owns a hole". However females occasionally "wing wave" which suggests that the behaviour is defensive.

Apparently European birds perform the same way. Schüz (1943) describes wing waving, and throat puffing. He also observed males crowing inside a box and bringing in green leaves.

The defensive behaviour begins in August, at least for some birds, increases till November, decreases in December, and then increases greatly from January to April. This seasonal change has been reported for a number of places: Faroe Islands (Williamson, 1947), England (Bullough, 1942; Marples, 1936; 1936b; Morley, 1939; 1941), Germany (Wallraff, 1953), Holland (Kluijver, 1933; 1935), and for *S. cineraceus* in Japan (Kuroda, 1955). The defence revives before renesting, and the vocabulary changes somewhat. From August to December the aggressive behaviour consists of weak crowing and partial wing-waving. In late December the intensity begins to increase till early April when screaming and full wing-waving occur.

The male ceases puffing and crowing when a female comes near. On many occasions after January the male stopped crowing when the female perched nearby or started crowing when she left.

The female also defends a nest hole from October till nesting but the aggressive behaviour is mild. Puffing may occur in March and April and real fighting just before laying. In several cases a vicious fight inside the box has been observed (Allard, 1940).

Aggressive behaviour of wild birds when feeding on bread on the ground is the same as that seen in caged birds. Generally when several birds are together a warning thrust of the bill forces a bird away.

Territorial Rank

There is no territorial behaviour of the "typic-

al" warbler or bunting type. Starlings do not select and defend an area of land in which the female will build. In contrast the males dominate a nest hole and drive other birds away. Birds of either sex may perch nearby in transit or feed on the ground but are not permitted near the hole while the owner is watching.

The females behave in essentially the same way, presumably all year but at least in spring when sex can be distinguished through binoculars. Commonly, females may fight within the nest hole. In one case (April 1957) two females fought for seven minutes inside a box. Although the birds were not visible they gave an assortment of screeches and squeals and pounded each other. Finally one bird burst out of the box and flew rapidly away. The other (who was the owner) followed a short distance and then perched.

The behaviour satisfies territorial criterion of exclusiveness but the patterns are the same as those shown in dominance in a cage. It is, of course, true that the same behaviour pattern may serve different functions, but the great similarity suggests that the starling dominates the birds that are close to it or to the nest hole. Since in nature a subordinate bird can leave the area, it does so and sets up a "rank" at another nest hole. Thus the whole breeding area is divided up into "groups" which have only one bird (the dominant one) because all the others have left. In this interpretation territorialism is a special case of social rank and is here called territorial rank.

Other authors have referred to territorial behaviour in starlings. Kluijver (1935) and Kessel (1957) were primarily interested in reproductive performance and referred simply to territorial behaviour. Schuz (1942) mapped territories and commented that the largest territories had a radius of five metres. His description agrees in almost every detail with the observations reported here, and he even reports that birds sleeping together in a box have a rank. Wallraff (1953) noted that "territorial" behaviour was inhibited by cloudy weather and described behaviour essentially identical to the type here reported.

Ownership of the hole is demonstrated by visits by the male and female. Table III shows days of regular observations (i.e. at least an hour

Table III. Visits to Box by Banded Male and by R W Female (1956-57)

Month	Days observed	Behaviour of the male				Behaviour of female	
		Hung	Enter	Twigs	Entice	Hung	Entered
Nov.	7	1	2	0	0	1	0
Dec.	9	2	0	0	0	0	0
Jan.	23	0	1	0	0	0	0
Feb.	11	4	5	1	0	5	0
March	15	13	3	3	3	3	5

Visits to Three Boxes by Several Males and Females (1957-58)

Sept.	11	0	5	1	0	0	0
Oct.	26	8	6	0	0	1	0
Nov.	30	7	9	0	0	0	4
Dec.	24	1	3	0	0	0	0
Jan.	31	0	1	0	0	0	0
Feb.	28	2	1	0	0	0	0
March	29	0	7	2	4	2	7

starting at dawn) and the visits to box by the banded male and by R W female. In November and December the birds merely hung on the front or entered. In January the bird entered the box only once while being observed. In February the visits increased and once the male brought in twigs. In March the entrances were almost daily and some building and enticing (with "whew" call) occurred. In April the visits and building occurred daily and enticing was frequent.

The table also gives data for the subsequent year for several birds at three boxes. Since different numbers of birds are involved in different months no rates can be calculated. However seasonal changes in frequency for both male and female are apparent.

The behaviour for renests is essentially the same as above except condensed into a few days. The male resumes wing-waving and crowing vigorously and lines the nest with green leaves. He solicits any female and entices her to the box. After the laying period the male reduces his activities to mere passive presence.

A puzzling difference occurs in the roosting habits during the winter of birds observed in the Baltimore area and the reports of roosting in Europe and New York State. A number of authors (Kluijver, 1933; 1935; Kessel, 1957; Schuz, 1942; Fitter, 1949) found that birds (males and females) roost in boxes or holes. However, no bird roosted in three boxes during two winters in a residential area 8 miles from downtown. Futhermore, no bird was found in about 40 boxes on three visits in February. The boxes are located in a woods about 12 miles from city roosts and birds fly towards the roosts at night and from in the morning. An explanation for this difference is not apparent.

Pairing

The analysis of pairing is seriously hindered by the impossibility of distinguishing sex till January unless the birds are captured. However, in January there is no evidence that birds are paired. A female, however, may own the same box as does a male. This curious distinction is based upon various observations. In one case a female (RW) defended two holes against all females from February to April before deciding on one hole. During all this time the males that owned each hole solicited all females that came along and attempted to entice each into the hole. Furthermore, after the first clutch was destroyed the banded male who was now the mate of RW solicited all females for several days but RW came back and drove a new female away. Many similar cases could be cited.

However, the pair from the first brood may remain together for a renest after destruction of the first nest. For example a pair nested in one hole and then took over another but when trapped deserted it.

The females may own a box as early as November and maintain it during the winter. The female tolerates the male at the box and may perch near the box as he goes inside. On several occasions in the fall one bird (presumably male) attempted to entice another to enter the box. However no clear pairing has been observed till April.

The defence by the female is so mild that very close attention is necessary to detect it. The best time to see the behaviour is about an hour after sunrise.

Apparently pairing does occur just before laying for suddenly two birds are regularly seen together. The birds feed on the lawn close together, fly off and perch near each other and fly off to the city together.

Some objective evidence is available from the numbers of doubles that are seen flying from the city where they roost at night. During most of the year the birds roost in the city (8 miles away) and return in scattered flocks the following morning. Table IV shows the results for April 1958. The number of "flocks" containing two birds suddenly increases and later many singles occur that are presumably the paired male whose female is incubating. The data from September 1957 through March 1958 are essentially the same as the data from 2-16th April. The increase in number of doubles on 17th April is clear. Presumably these are now paired rather than simply two birds flying along together. An egg was found on the ground on 19th April and the first egg laid in 60 boxes was deposited on 20th April. The drop in proportion of doubles on 22nd April is presumably due to the initiation of incubation by the females at night.

The same phenomenon occurred in the evening but for practical reasons it was difficult to get quantitative data. Regularly after 17th April a pair was observed sitting together on a branch near a box. After one-half to one hour the female would suddenly fly off toward the city and the male would follow. In all the cases that the sex could be identified the female led. In the morning the birds did not necessarily return together although many pairs did. After incubation began the male flew towards the city alone.

Table IV. The Proportion of Flocks that were "Doubles" During April, 1958

April	Flocks	Proportion
2	17	·12
3	35	·26
4	23	·17
5	24	·17
7	21	·19
8	34	·15
9	24	·17
10	35	·08
14	22	·14
15	23	·17
16	32	·32
17	30	·33
18	51	·31
19	43	·42
20	38	·42
21	14	·39
22	17	·06
23	30	·23
24	15	·20
25	35	·11
26	30	·20

The conclusion that pairing occurs in the spring agrees with Kluijver (1935) who reported that pairing occurred late in spring even though in some cases a male and a female were found together in a box in February. Schuz (1942) reported that birds did not pair in the fall.

An unresolved problem is a behaviour pattern consisting of a rapid flight of one bird after another. The birds may turn and twist rapidly among the tree tops and back to the ground. The difficulty is that the sex can rarely be determined and sometimes three birds participate. Bayne (1933) called it a sexual chase but did not know the sex of the birds. In 1958 it was first observed on 24th March and became frequent around 15th April. Although many chases have been observed, sex could be determined in only a few cases. Twice the anterior bird was a banded female; once the posterior bird was a male; once the anterior bird was mounted by the posterior bird. Once a banded male chased a female. From these observations it seems that this behaviour really is a sexual chase; a possible function is to drive the female to the box since it occurred in birds not yet paired. (Copulation between paired birds was not preceded by this chasing).

The History of "Warbler"

The observations described above have dealt with several birds and given as much quantitative data as possible. However, it seems likely that a more comprehensible and vivid understanding can be obtained by following the history of one male. A bird, called "Warbler" from his characteristic notes, provides a variety of illustrations of behaviour.

Warbler first appeared on 15th November, 1957, at 0644 hours and crowed vigorously at a hole in an oak tree. He was very obviously a stranger as demonstrated by hopping from perch to perch and frequent exploring. Later on (0730 hours) he entered a box (G). On 16 November at dawn he appeared in the oak and crowed but soon moved over to a maple near box G and began his unique warble (Since the bird was not banded there is no proof that this was the same bird. However, the behaviour was so distinctive that there is no doubt). For an hour Warbler fought with a bird and attempted to get a female to follow him into the G box. A banded bird (Black) who owned box B was an interested spectator. From 17-20 November Warbler was present near the G box and entered several times, but on 21 November he began to fight with male B at Box B. Both birds crowed vigorously and eventually grappled and fell to the ground. B disappeared and was never seen after that fight.

For the next month Warbler regularly visited Box B. He sometimes went into the big oak or over near box G. On several occasions other males appeared but were driven away. Also females came and went. By the middle of December Warbler had a regular routine for arrival. Each morning when he came from the city, he landed in the top of a spruce. There he warbled for 5-10 minutes before going over to check his box. In December he drove away at least three males from his box. His bill was partially yellow but by February it was possible to see clearly the blue base to the bill.

In early March Warbler solicited females more actively. He "wing-waved" vigorously, gave the "whew" call when females came close and on several occasions warbled persistently at a female that was near the nest box. Also during early March he began to defend other holes occasionally when a female came near the holes. On 9 March he followed a female into G box and both birds were trapped (and banded). He did not go near G box after that experience but stayed at B. Another male took over G. On numerous occasions he drove away one or even two males from his box. In early April he regularly occupied the hole in the oak which formerly belonged to another male which had disappeared. However, by 10 April Warbler was again regularly defending box B. On 16 April at 0530 hours Warbler chased a bird around the area in rapid flight and eventually returned to B and warbled. At 0730 hours an unbanded female went into box B while Warbler watched (She was not trapped to

avoid desertion). On 16 April a banded female entered B box while Warbler watched and then flew off followed by him. Later the two birds were seen on the ground together. Nothing noteworthy occurred on 17 and 18 April but on 19 April an unbanded female was trapped in B box and Warbler drove a male from the box. On 21 April he drove another male from the box. He was present on 22 and 23 April and on 24 April enticed into box B a female which was trapped. On 25, 26, and 27 April an unbanded male was present in B several times, but was driven out by Warbler. On 29 April a female entered B box and Warbler brought in some leaves. He then chased her in flight, copulated and chased again. In the late afternoon she entered the box several times and also copulated. On 30 April he was captured and autopsied. The testes were medium size and sperm were present in the seminal glomus.

To summarize this male's history very briefly, it seems clear that he defended a hole until a female chose it.

Discussion

The observations here reported show that starlings behave aggressively in the wild the same as in captivity. The big difference seems to be that subordinate birds can flee in the wild but not in captivity. Indeed the behaviour of birds roosting in the city at night is apparently identical to that of birds in captivity. Thus, it appears that the starling has a social rank in the wild but the subordinate individuals are present only temporarily, and thus we have a superficial resemblance to territorial behaviour. Indeed, one may postulate that territorial behaviour is simply social rank without subordinates. A somewhat similar situation occurs in mice (Crowcroft, 1955; Davis, 1958) that may be territorial at low density of population but arranged in a rank at high density. The observations here presented on starlings agree with the hypothesis that a continuum exists from situations that are exclusively territorial at one extreme to those that are exclusively rank. For example, Mockingbirds are territorial for practically the entire year and apparently never form a social rank, whereas sage grouse are always ranked and never defend a territory. At various places on this continuum are other species such as cardinals, manikins, gulls and starlings.

Summary

The starling (*Sturnus vulgaris*) presents some unusual aggressive behaviour patterns that may clarify the relation of territorial behaviour to rank behaviour. Birds were observed (600 hours) under natural conditions throughout the year at nest boxes. In addition birds in large cages were examined. The vocabulary is varied. The male has two aggressive calls and three calls to attract the female. In addition each male has an individual song and of course alarm and flock calls. The female has several calls as well as the alarm and flock calls.

The aggressive behaviour in captivity consists of "crowing" and puffing the throat while the birds are perched side by side. This occurs in the absence of a nest box and occasionally may culminate in a fight. In wild birds the same behaviour occurs at various places but usually near a box.

"Wing-waving" is a means of advertisement to a male or to a female that the nest hole belongs to a bird. Defensive behaviour begins in September and is maintained at low intensity till March. It increases before pairing in April and then declines. Pairing occurs about five days before laying.

No territorial behaviour of the conventional kind has been observed. The males and females drive other males away from nest holes in the same manner that is used to establish rank in cages. From this evidence it is suggested that territory is really a special case of social rank.

REFERENCES

Allard, H. A. (1940). The starling's family life and behaviours. *J. Wash. Acad. Sci.*, **30,** 34-46.

Bayne, C. S. (1933). The sexual chase among starlings. *Brit. Birds*, **27,** 104-106.

Bennett, Mary G. (1942). Effect of testosterone propionate on territoriality in flocks of ring doves. *Trans. Ill. Acad. Sci.*, **193-194.**

Bullough, W. S. (1942). The reproductive cycles of the British and continental races of the starling. *Phil. Trans. B.*, **231,** 165-246.

Crowcroft, P. (1955). Territoriality in wild house mice, *Mus musculus*. L. *J. Mamm.*, **36,** 299-301.

Davis, D. E. (1957). Aggressive behaviour in castrated starlings. *Science*, **126,** (3267), 253.

Davis, D. E. (1958). The role of density in aggressive behaviour of house mice. *Anim. Behav.*, **6** (3 & 4), 207-210.

Dunnet, George M. (1955). The breeding of the starling *Sturnus vulgaris* L. in relation to its food supply. *Ibis*, **97** (4), 619-661.

Fabricius, E. & Karl-Jokob Gustafson (1954). Further aquarium observations on the spawning behaviour of the Char, *Salmo alpinus* L. *Inst. Fresh-Water Res. Rept.*, **34,** 58-104.

Hilton, F. K. (1958). Behavioural and biochemical aspects of the yearly gonadal cycle in male starlings. *Sc.D. Dissertation, Johns Hopkins University.*

Fitter, R. S. R. (1949). *London's birds*. London: Collins, p. 1-256.

Kessel, Brina (1957). A study of the breeding biology of the European starling *Sturnus vulgaris* L. in North America. *Amer. Mid. Nat.*, **58** (2), 257-331.

Kluijver, H. N. (1933). Bijdrage tot de biologie en de ecologie van den spreeuw *Sturnus v. vulgaris* gedurende zjin voortplantingstijdVersl. en Meded. *Plantenziektenk, Dienst, Wageningen*, **69,** 1-146.

Kluijver, H. N. (1935). Waarnemingen over de Levenswilze van den Spreeuw *Sturnus v. vulgaris* met Behulp van geringde Individen. *Ardea*, **24**, 133-166.

Kuroda, Nagahisa (1955). Field studies on the gray starling *Sturnus cineraceus* Temminck. I. From winter to breeding season. *Misc. Rep. Yamashima's Inst. Ornith. Zool.*, **7**, 277-289.

Marples, G. (1936). Starlings fighting for nesting sites. *Brit. Birds*, **29**, 321-323.

Marples. G. (1936 b). Behaviour of starlings at the nesting site. *Brit. Birds*, **30** (12), 14-21.

Morley, Averil (1939). Rising and roosting of a pair of resident starlings in winter and early spring. *Brit. Birds*, **33**, 39-43.

Morley, Averil (1941). The behaviour of a group of resident British starlings *Sturnus v. vulgaris* L. from October to March. *Naturalist*, **788**, 55-61.

Schuz, E. (1942). Biologische beobachtungen an Staren in Rossitten. *Der Vogelzug*, **13** (3-4), 99-132.

Schuz, E. (1943). Brutbiologische Beobachtungen an Staren 1943 in der Vogelwarte Rossitten. *J. Ornith*, **91** (4), 388-405.

Wallraff, H. G. (1953). Beobachtungen zur Brutbiologie des Stares *Sturnus v. vulgaris* L. in Nurnberg. *J. Ornith.*, **94** (1-2), 36-67; **B.A. 27**, 26649.

Williamson, K. (1947). Field Notes on the Faeroe Starling. *Ibis*, **89**, 435-439.

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THE DEVELOPMENT OF NESTING BEHAVIOUR IN THE SIAMESE FIGHTING FISH *Betta splendens*

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Introduction

Males of the Siamese Fighting Fish *Betta, splendens*, build bubble nests. A bubble of air is taken into the mouth, enclosed in mucus, and deposited on the surface of the water. This is repeated until an aggregation of mucus-covered bubbles is present. Mating follows, and the male catches the eggs in his mouth and deposits them in the nest where they remain until hatching and for some time thereafter. Eggs and young fish, which continually fall from the nest, are caught as they slowly sink and are returned to the bubble nest. The male also continually adds bubbles to the nest, replacing those that have burst and often materially increasing the size of the nest.

The literature concerning the reproductive behaviour of *B. splendens* is surprisingly meager when one considers that the species has long been known as a recreational oddity in Thailand and has been domesticated there for at least 100 years (Smith, 1945) and perhaps much longer (Forselius, 1957) and has also been a popular aquarium fish in Europe and the United States for at least 30 years. Most of the so-called information is of the "popular" variety and much of it is entirely erroneous. The principal scholarly studies are those of Regan (1909) who identified the species, Lissmann (1932) who published significant information concerning its stimulus-response system but devoted very little space to reproductive behaviour, Smith (1937, 1945) who presented a good, general account of the behaviour and general ecology of the fish, and Forselius (1957) who published an exhaustive ethological study of the family Anabantidae including much information concerning the reproductive behaviour of a number of species. An outstanding characteristic of the above-cited literature is the lack of agreement among, and even within, reports. For instance Smith (1945) stated that female *B. splendens* do not build nests, while Forselius (1957) indicated that they do and have even been observed to care for young in them. He lists this under "pseudo-male" behaviour, however, which indicates that he does not consider such activity characteristic of the female. The reports also contain disagreement concerning the functions of the nest both with regard to the nurturing of the young and as a releaser of adult behavioural patterns. Both Smith and Forselius (*op. cit.*) stated that the females co-operate with the males in placing eggs in the nest. We have observed in excess of 150 matings and have never noted this activity on the part of the females. The present work was undertaken, in part, to attempt to clear up some of the existing confusion concerning the nesting activity of the females.

Forselius (*op. cit.*) reported that nesting activity among the Anabantidae either accompanies or occurs immediately after the appearance of secondary sexual characteristics both of anatomy and behaviour. Thus nesting behaviour should be a good indication of sexual readiness in the male. Also, fully adult males breed only in the presence of a nest; in its absence they may attack the female or, probably stimulated by her presence, build one.

Using *Colisa lalia* as his test animal, Forselius was able to observe that nesting activity in that species develops in correlation with anatomical, physiological, and behavioural maturity but that there is great variation among individuals with regard to the age at which the first nest is built. This work represents an attempt to learn at what age nesting behaviour first appears in both sexes of *B. splendens*, the relative frequency in each sex, and the relative frequencies at various ages. The nests themselves were also studied with regard to shape, size, thickness, and duration.

Methods and Materials

The fish whose nesting activities are recorded here were all bred in a small laboratory of the Department of Zoology at Michigan State University. A description of the physical arrangements of this room appears in an earlier paper (Braddock & Braddock, 1955).

A total of 154 individuals was involved in these observations. Seventy-four were males and 80 were females. The uneven sex ratio occurred because the observations were begun when the fish were too young to be sexed. They were selected from five litters, all of different parent-

age as follows: *Litter* 1 consisted of 48 individuals of which 21 were males and 27 were females; *Litter* 2 contained 42 fish, 23 males and 19 females; *Litter* 3 was made up of 9 individuals, 5 males and 4 females; *Litter* 4 consisted of 31 fish of which 15 were males and 16 females; and *Litter* 5 consisted of 10 males and 14 females, 24 in all. The data were originally tabulated according to the five litters but are grouped as presented here since no significant differences were noted among them.

Certain environmental conditions were the same for all of the individuals. All were hatched in 20-gallon aquaria in the laboratory, and all were maintained in aged tap water throughout the entire period of observation. The temperature of the room never fell below 80°F., although the upper limit varied as much as 4°F. Fans kept the temperature relatively equal throughout the room; so that it is probable that all of the fish were in water of approximately the same temperature at any given time. Light was supplied by overhead fluorescent lamps and natural daylight. The lamps were turned off at night. From the time when they were removed from the aquaria in which they were hatched until the observations were concluded each individual was housed separately in a one-gallon, glass jar approximately two-third full of aged tap water.

The feeding procedure was uniform for all of the fish. They were fed infusoria (from a rich culture of Protozoa and rotifers) from the time of hatching until they were seven days old. The feeding of infusoria was continued during days 8-14 but was supplemented with newly-hatched brine shrimp. Brine shrimp were given exclusively on days 15-56. From the fifty-seventh day on the fish were given brine shrimp plus finely ground commercial shrimp.

The variable conditions concerned the amount of contact, visual and actual, with other individuals. All of the young fish remained in the aquaria in which they were hatched until they were at least two days old. Until they reach this age young Bettas are helpless and must be maintained in the nest by the male parent. After the second day post-hatching they begin to swim about and are able to care for themselves.

Nineteen males and nineteen females were removed from the aquaria in which they were hatched when they became free-swimming at two or three days of age. At this time each was isolated in a one-gallon jar, and the jars were covered in such a way that the fish were also visually isolated. All remained under these conditions until they were at least 55 days of age. Four males and six females were temporarily removed from visual isolation for testing in other observations at 55 days. At 69 days five males and five females were similarly tested, while three males were removed for testing at 70 days. Six males and seven females were tested at 77 days; one male and one female at 83 days. After testing all of these fish were again isolated in jars but complete visual isolation was not universally maintained. Thus, they are treated as visual isolates only for the initial period mentioned above.

The other fish were all kept in the aquaria in which they were hatched until they were at least 18 days of age. Thereafter they were treated approximately as the group mentioned above. Although some were placed in visual isolation for varying periods of time, none are rated under that heading since they all had considerable visual contact with members of their own species after they became free-swimming at two or three days of age. This group was composed of 55 males and 61 females.

Observations were begun as soon as the fish were placed in individual containers (3-68 days post-hatching) and were made daily, usually between 8 and 10 a.m., until terminated. All litters except number 3 were observed until 365 days; for Litter 3 the time was 300 days post-hatching. Records were continued past the official termination dates for nests present at the time in order accurately to determine their duration.

The numbers of individuals suffered attenuation as the observations progressed. Deaths occurred, and fish were removed, either temporarily or permanently, for testing in connection with other problems. Adjustments to cover this situation have been made in the tables that follow.

Where individuals were physically, but not visually, isolated a record was kept of the neighbours that could be seen by each. The containers were arranged in such a manner that the following permutations were possible; two neighbours, both males; two, both females; one, male; one female; and none. The numbers were too small for adequate statistical comparison of possible effects of the various combinations, but nests were built in all of them.

Whenever a nest was present that fact was recorded along with its size, shape, thickness, compactness, and position in the container.

Since the nests could not be measured directly without danger of damaging them, a set of patterns of known area and based upon the shapes of actual nests was used. Each nest was matched to the closest pattern, and its area was recorded as that of the pattern. In the tables that follow the presence of nest bubbles is recorded as evidence of nesting activity regardless of the amount except where otherwise specified.

The shapes recorded were as follows: small sections of broken strings of bubbles, bubbles scattered over the surface of the water, a complete line of bubbles around the circumference of the jar with intermittent thickenings, very small crescent-shaped or round nests, and larger nests that were usually roughly crescent-shaped, probably due primarily to the round shape of the jars.

A record was also kept of the age at which each fish built its first nest, the number of nests built by each, the amount of time each spent in nesting activity, the type of nests each built, and the duration in days of each nest.

In presenting our data the primary emphasis will be upon a comparison of the relative amounts of nesting activity displayed by males and females generally and at various ages.

Nesting Activities, Males and Females

Since the fish whose activities are recorded here were all sexually immature at the start of the observations, it was possible to record the time of inception of nesting for each individual, and to make comparisons between males and females (Table I). It should be noted that for the purposes of this table the presence of any appreciable number of nest bubbles over a period of one or more hours was recorded as a nest. The data are presented according to 14-day periods, and, for each period, individuals that died or were removed permanently or temporarily from the project for any reason are omitted.

Comparison of the information presented in Table I indicates that the males began nesting at an earlier age than the females. Approximately 17 per cent. of the males built their first nests prior to 66 days of age, while none of the females had done so at that time. At the age of 108 days 58 per cent. of the males had built nests and only 7 per cent. of the females. By the 290th day 95 per cent. of the males were accounted for and only 55 per cent. of the females.

Since 95 per cent. of the males and 97 per cent. of the females had produced nest bubbles before the observations were terminated, it may be in-

Table I. Ages at which First Nest Bubbles were Recorded.

	Males				Females			
Age in days	number indiv. observed	number built 1st nests	% built first nests	cumul. % built 1st nests	number indiv. observed	number built 1st nests	% built first nests	cumul. % built 1st nests
53—66	65	11	16·9	16·9	71	0	0·0	0·0
67—80	74	12	16·2	33·1	79	0	0·0	0·0
81—94	74	8	10·8	43·9	77	3	3·9	3·9
95—108	71	10	14·1	58·0	75	2	2·7	6·6
109—122	69	6	8·7	66·7	71	1	1·4	8·0
123—136	64	1	1·6	68·3	68	1	1·5	9·5
137—150	57	2	3·5	71·8	67	3	4·5	14·0
151—164	56	2	3·6	75·4	65	3	4·6	18·6
165—178	53	0	0·0	75·4	65	1	1·5	20·1
179—192	54	2	3·7	79·1	63	3	4·8	24·9
193—206	47	3	6·4	85·5	61	1	1·6	26·5
207—220	48	1	2·1	87·6	62	2	3·2	29·7
221—234	46	1	2·2	89·8	60	3	5·0	34·7
235—248	43	0	0·0	89·8	57	4	7·0	41·7
249—262	40	0	0·0	89·8	54	2	3·7	45·4
263—276	39	0	0·0	89·8	53	3	5·7	51·1
277—290	37	2	5·4	95·2	50	2	4·0	55·1
291—304	33	0	0·0	95·2	45	4	8·9	64·0
305—318	32	0	0·0	95·2	41	6	14·6	78·6
319—332	31	0	0·0	95·2	39	3	7·7	86·3
333—346	28	0	0·0	95·2	36	4	11·1	97·4
347—360	25	0	0·0	95·2	32	0	0·0	97·4

ferred that the activity is practically universal in both sexes.

The information presented in Table I also defines the developmental period for nesting activity in both sexes. Thus the last male to build its first nest did so when it was between 277-290 days of age and the last female between 333-346 days. This, coupled with the previously mentioned fact that nesting behaviour was almost universal by the 290th day for males and the 346th day for females, appears to define the period of development for males approximately 53-290 days and for females as 81-346 days.

Table II presents data regarding the proportionate amounts of time spent in nest building and maintenance by males and females of various ages. This is expressed in terms of the number of days nest bubbles were present for each fish in each 14-day period. Since adjacent periods tended to show little difference, summaries of groups of five such periods (70 days) are given as separate columns.

It is immediately apparent that nesting activity increased for both sexes as time passed. The mean number of nesting days per male was 1·9 for the period covering days 53-122, 5·6 days 123-192, 6·8 for days 193-262, and 9·7 for days 263-332. Comparable figures for the females were: 0·1, 0·8, 2·6 and 4·7. It is also clear that the males engaged in the greater amount of nesting activity at any given age within the range of these observations.

Table II also shows that male nesting activity accelerated rapidly during the early stages of the observations (1·3 - 6·2 days/individual/14 - day period during days 53-150) and that this was in sharp contrast to that of the females (0·0-0·7) during the same period. Between days 150-262 the males exhibited a gradual increase followed by a marked acceleration toward the end of the observations. On the other hand the increase in female nesting activity may be described as more gradual throughout.

The suggestion may be made that the quantitative differences in male and female nesting activity recorded for these observations may be entirely the result of the fact that the males started earlier. To this may be added the factor of more rapid acceleration in the case of the males, especially during the earlier stages of the observations. Thus, since most of the information recorded here concerns the developmental

Table II. Number of Days Upon which Nests Occurred at Various Ages.

	Males				Females			
Age in days	number indiv. observed	total nest days	$\bar{v}$ days maintenance/fish	cum. $\bar{v}$ maint. 5 per.	number indiv. observed	total nest days	$\bar{v}$ days maintenance/fish	cum $\bar{v}$ maint. 5 per.
53—66	65	84	1·3		71	0	0·0	
67—80	74	107	1·4		79	0	0·0	
81—94	74	121	1·6		77	7	0·1	
95—108	71	169	2·4		75	26	0·3	
109—122	69	192	2·8	1·9	71	19	0·3	0·1
123—136	64	276	4·3		68	10	0·1	
137—150	57	352	6·2		67	47	0·7	
151—164	56	334	6·0		65	77	1·2	
165—178	53	308	5·8		65	57	0·9	
179—192	54	319	5·9	5·6	63	79	1·3	0·8
193—206	47	305	6·5		61	105	1·7	
207—220	48	276	5·8		62	131	2·1	
221—234	46	320	7·0		60	151	2·5	
235—248	43	322	7·5		57	175	3·1	
249—262	40	285	7·1	6·8	54	188	3·5	2·6
263—276	39	331	8·5		53	215	4·1	
277—290	37	356	9·6		50	223	4·5	
291—304	33	329	10·0		45	180	4·0	
305—318	32	313	9·8		41	202	4·9	
319—332	31	326	10·5	9·7	39	234	6·0	4·7
333—346	28	320	11·4		36	229	6·4	
347—360	25	241	9·6		32	249	7·8	
361—374	14	156	11·1		15	141	9·4	
375—388	9	119	13·2		11	134	12·2	
389—402	5	66	13·2	11·7	4	38	9·5	9·1

period for the activity, these differences may not reflect the situation in fully adult Bettàs.

One cannot resolve this problem merely by noting that the curves representing male and female nesting activity are still far apart after all individuals have built their first nests. If the amount of activity remained constant after it was once begun, this difference might be expected to persist. If, however, individuals increased their activity until a maximum was reached, and this was the same for both sexes, the curves would eventually meet. A third alternative is that increase might occur but that the maxima would be different for males and females. Table III deals with the problem of whether increased nesting activity may be explained solely on the basis of the addition of more nesting individuals as time passed.

The "nesting" fish recorded in Table III include not only those individuals that exhibited such behaviour during each 14-day period but also all those that had nested previously and were present during the period under consideration. They might also be called potential nesters. In each case the total number of days spent in nesting activity by all of the fish present was divided by the total number of potential nesters present. If the resulting figures were the same, or nearly so, for all of the 14-day periods, one could conclude that the increasing nesting activity noted in Table II was solely the result of the continual addition of more individuals capable of nesting as time progressed.

The treatment of the data in Table III eliminated the effect of the addition of new nesting fish as the observations progressed. Under these circumstances it is apparent that there was still an increase in the amount of time devoted to nesting as the fish grew older. This was true for both sexes. Therefore, it can be concluded that the individuals increase the proportionate amount of their time spent in nesting after they have begun the activity. The figures presented in Tables II and III naturally approach more closely to each other as time passes, since the continual addition of fish that have demonstrated their nesting ability gradually eliminates that factor from Table II until after 290 days for males and 346 days for females it is gone entirely.

When males are compared with females with

Table III. Number of Days Upon which Nests Occurred at Various Ages. Fish which had never nested excluded.

	Males				Females			
Age in days	No. nesting indiv. observed	Total nest days	$\bar{v}$ days maintenance per nesting fish	cum. $\bar{v}$ maint. 5 per.	No. nesting indiv. observed	Total nest days	$\bar{v}$ days maintenance per nesting fish	cum. $\bar{v}$ maint. 5 per.
53—66	11	84	7·6		0	0	0·0	
67—80	23	107	4·7		0	0	0·0	
81—94	31	121	3·9		3	7	2·3	
95—108	41	169	4·1		5	26	5·2	
109—122	47	192	4·1	4·9	6	19	3·2	2·1
123—136	46	276	6·0		6	10	1·7	
137—150	44	352	8·0		10	47	4·7	
151—164	45	334	7·4		11	77	7·0	
165—178	43	308	7·2		12	57	4·8	
179—192	46	319	6·9		14	79	5·6	4·8
193—206	43	305	7·1		16	105	6·6	
207—220	45	276	6·1		19	131	6·9	
221—234	45	320	7·1		21	151	7·2	
235—248	41	322	7·9		24	175	7·3	
249—262	38	285	7·5	7·1	24	188	7·8	7·2
263—276	37	331	8·9		26	215	8·3	
277—290	37	356	9·6		27	223	8·3	
291—304	33	329	10·0		25	180	7·2	
305—318	33	313	9·5		29	202	7·0	
319—332	32	326	10·2	9·6	30	234	7·8	7·7
333—346	30	320	10·7		31	229	7·4	
347—360	27	241	8·9		29	249	8·6	
361—374	14	156	11·1		16	141	8·8	
375—388	9	119	13·2		12	134	11·2	
389—402	5	66	13·2	11·4	4	38	9·5	9·1

regard to the increase in nesting time per individual, it is apparent that the former still have a head start on the latter and remain ahead throughout most of the developmental period. Also, the degree of difference between the sexes reflects the rapid increase in general nesting activity exhibited by the males during the early stages of the observation period, the gradual increase during the middle phase, and the acceleration toward the end as well as the more general increase shown throughout by the females.

The developmental patterns of the male and female groups suggest that their curves would have approached each other more closely as they grew older, since the females exhibited a slower increase in nesting activity than the males and could thus be expected to continue after the males had become stabilised. While these data do not indicate whether or not the amount of female nesting activity would ever have been equal to that of the males, they suggest that the difference would eventually have been small.

Nature of Male and Female Nests

As previously treated in this work nesting behaviour has been defined simply as the production of nest bubbles. Actually, reproductive success involves the ability of the male to produce a nest of a size greater than the critical minimum before mating and to maintain it for a sufficient period of time afterwards. In addition, while our observation of more than 150 successful matings has indicated that the actual shape of the nest is not critical to its success, it must be compact rather than a linear series of bubbles.

Table IV deals with the numbers of nests of various durations and indicates that the nests built by males varied from less than one day to 160 days while those built by females ranged from less than one day to 140 days. In both sexes

Table IV. Duration of Nests: Consecutive Number of Days Maintained.

	Males			Females		
Number of days duration	Number of nests	%	cumulative %	Number of nests	%	Cumulative %
1	93	16·3	16·3	33	12·2	12·2
2	72	12·7	29·0	41	15·1	27·3
3	61	10·7	39·7	25	9·2	36·5
4	46	8·1	47·8	29	10·7	47·2
5	36	6·3	54·1	20	7·4	54·6
6	28	4·9	59·0	19	7·0	61·6
7	16	2·8	61·8	9	3·3	64·9
8	16	2·8	64·6	10	3·7	68·6
9	20	3·5	68·1	2	0·7	69·3
10	14	2·5	70·6	8	3·0	72·3
11	15	2·6	73·2	7	2·6	74·9
12	12	2·1	75·3	3	1·1	76·0
13	15	2·6	77·9	5	1·8	77·8
14	8	1·4	79·3	5	1·8	79·6
15	11	1·9	81·2	3	1·1	80·7
16	7	1·2	82·4	2	0·7	81·4
17	6	1·1	83·5	4	1·5	82·9
18	6	1·1	84·6	5	1·8	84·7
19	1	0·2	84·8	2	0·7	85·4
20	3	0·5	85·3	2	0·7	86·1
21—30	29	5·1	90·4	12	4·4	90·5
31—40	21	3·7	94·1	6	2·2	92·7
41—50	10	1·8	95·9	6	2·2	94·9
51—60	5	0·9	96·8	4	1·5	96·4
61—70	6	1·1	97·9	1	0·4	96·8
71—80	2	0·4	98·3	3	1·1	97·9
81—90	4	0·7	99·0	1	0·4	98·3
91—100	0	0·0	99·0	2	0·7	99·0
101—110	1	0·2	99·2	0	0·0	99·0
111—120	1	0·2	99·4	0	0·0	99·0
121—130	1	0·2	99·6	1	0·4	99·4
131—140	1	0·2	99·8	1	0·4	99·8
141—150	0	0·0	99·8	0	0·0	99·8
151—160	2	0·4	100·2	0	0·0	99·8

most of the nests lasted five days or less; and the median was approximately five days. It may be useful to note that this is the time a nest must last to insure reproductive success. The eggs require about two days to hatch, and the young do not become independent until two or three days after hatching.

An attempt was made to correlate nest duration with age, but no correlation was discovered. Nests of both long and short duration were built by individuals of all of the ages covered by these observations, and young fish exhibited no tendency to build more than their share of the shorter-lived nests or vice versa. In addition the distribution of the nests built by the females was not significantly different from that of the males. Finally, no evidence was uncovered that would indicate that certain individuals tended to specialise in nests of a particular duration.

The principal importance of the above is probably the fact that individuals of both sexes, in the absence of another fish, exhibited the ability to maintain nesting activity for considerable periods of time. Whether this was intermittent, as was the case when a series of nests of short duration was built, or continuous, is probably of little importance, since an adequate nest can be built in 45 minutes. It should also be noted that continuous nests of long duration varied greatly in size from day to day. In the case of the males the tendency to produce a series of nests in the absence of a female is of obvious adaptive significance, since it reduces the time preliminary to mating when a female appears. Also, it is possible although not known, that the nest acts as a mating stimulus to the female. (Forselius, 1957). The possible significance of female nesting behaviour will be treated in the discussion section of this paper.

Table V records the number of days both sexes spent in maintaining nests of various sizes. The larger examples (5 $cm.^2$ and over) were almost all built by males. Since our numerous previous observations of the mating procedure in this species have indicated that a nest must have a minimum area of approximately 6 $cm.^2$ to insure successful rearing of the young fish, the females are eliminated as playing an essential role in the nesting process.

A majority of the nesting days of the males was spent in maintaining nests of inadequate size. This should not be interpreted, however, as evidence of inability to build effectively. There were numerous instances where the nest of a particular male varied from extremely small to extremely large size on successive days or even during one day; in fact, this necessitated recording the largest size reached on each day in order to have consistency in tables concerned with nest size. Since all of these nests were built in tightly covered jars under controlled physical conditions, it is doubtful that these size variations depended on anything other than the activities of the fish themselves. The important fact is that the males demonstrated their ability to build useful nests, while the females did not.

Table VI is concerned only with those individuals that produced nest bubbles. It shows what percentage of the nesting fish had demonstrated their ability to construct adequate nests as various ages were reached. An area of 6 $cm.^2$ was selected as the minimum, and all nests of that or greater area were recorded. It will be noted that the percentage of successful nest builders became less on certain successive periods (e.g. 165-178 and 179-192 days). This resulted from the addition of bubble producers whose nests were of inadequate size at a faster rate than that for the increase in individuals building effective nests.

Reference to Table VI indicates that there was a marked increase in the proportionate number of males that had demonstrated their ability to build effective nests during days 53-150. At all times during this period the numbers of effective nesters were smaller than those of all bubble producers, but the former were increasing at a faster rate than the latter. Thus, up to this age there was an increasingly marked tendency for the older males to produce adequate

Table V. Relative Amounts of Time Spent Maintaining Nests of Various Sizes.

size in $cm.^2$	number of nest days	%	number of nest days	%
0·25—1·75	3164	48·4	2948	94·5
1·76—5·00	1498	22·9	168	5·4
5·01—16·50	1367	20·9	4	0·1
16·51—33·00	423	6·5	0	0·0
33·01—56·50	82	1·3	0	0·0
56·51—65·00	4	0·1	0	0·0

nests. During days 151-290 additional bubble producers and builders of adequate nests both appeared but at approximately the same rate. This indicates that after the fish had reached 150 days of age, additional age was a factor of small, if any, importance in producing fish capable of building the larger nests. After 290 days no additional individuals appeared in either category. In the case of the males this was the result of the removal of 13 individuals because of death or for other causes and represents 100 per cent. incidence of bubble production among the others. The 11 bubble producers that were never observed to build adequate nests might have done so in the presence of a sexually ready female or other outside stimulation. There is no evidence concerning this.

Table VI also clearly indicates the unimportance of female nesting activity. Only one female ever built a nest of adequate size and this only at an age greater than 361 days, long past the optimum mating age for this species.

The Effect of Visual Isolation

None of the females were visually isolated until or beyond the age at which their first nests appeared, and therefore these records contain no information concerning a possible effect of this treatment upon the amount of their nesting activity. As previously described, nineteen of the males were placed in visual isolation at two-three days of age and were removed from this condition at ages varying from 55-83 days. If they had been left longer, much useful information might have been gained, and further work will be attempted along these lines. During the age period of 53-66 days the 15 visual isolates that were present throughout constituted 24·6 per cent. of all the individuals under observation, and they accounted for 14 days of nesting activity or 17·3 per cent. of the total. Three of them built nests, while eight of the 46 non-isolates did so. Thus, during this earliest period of male nesting activity the participation of the isolated individuals was comparable to that of the others. The important fact is that visual isolation does not prevent nesting activity in young males.

Discussion

It seems probable that the evolution of bubble-nest building in the family Anabantidae was made possible in part by the air-breathing mechanism of these fish. This consists of a pair of cavities lined with vascular epithelium located in the sides of the head above the gills (Smith, 1945; Forselius, 1957). The fish frequently come to the surface of the water, expel the air from the labyrinth, and gulp a bubble of fresh air. This

Table VI. Time of Incidence of Effective Nests (6 cm.^{2} and larger).

Age in days	No. nesting indiv. cumulative	No. built effective nests. cum.	% effective nests cum.	No. nesting indiv. cumulative	No. built effective nests cum.	% effective nests cum.
53—66	11	3	27·3	0	0	0·0
67—80	23	6	26·1	0	0	0·0
81—94	31	12	38·7	3	0	0·0
95—108	47	16	39·0	5	0	0·0
109—122	47	26	55·3	6	0	0·0
123—136	48	32	66·7	7	0	0·0
137—150	50	41	82·0	10	0	0·0
151—164	52	44	84·6	13	0	0·0
165—178	52	44	84·6	14	0	0·0
179—192	54	45	83·3	17	0	0·0
193—206	57	48	84·2	18	0	0·0
207—220	58	48	82·8	20	0	0·0
221—234	59	48	81·4	23	0	0·0
235—248	59	48	81·4	27	0	0·0
249—262	59	48	81·4	29	0	0·0
263—276	59	49	83·1	32	0	0·0
277—290	61	50	82·0	34	0	0·0
291—304	61	50	82·0	38	0	0·0
305—318	61	50	82·0	44	0	0·0
319—332	61	50	82·0	47	0	0·0
333—346	61	50	82·0	51	0	0·0
347—360	61	50	82·0	51	0	0·0
361—374	61	50	82·0	51	1	2·0

almost precisely duplicates the bubble-blowing process. Only the addition of mucus is required to complete it. Forselius (*op. cit.*) also considers that the habit of eating unfertilised or damaged eggs may have been involved. The above, plus an environment with a stagnant, heavily-silted bottom may have made bubble-nest building both possible and adaptive.

The significance of the nest may be discussed under three headings: significance to the eggs and fry, significance to the adult male, and significance to the adult females. Forselius (*op. cit.*) has suggested that the nest plays an obvious and important role in keeping the eggs and fry together and thus facilitating nurture. A sufficient supply of oxygen is insured, and the same author reports that the male increases the thickness of the nest by adding bubbles from beneath after the eggs are placed in it. This is supposed to lift the eggs above the surface of the water where oxygen is more plentiful. Forselius also suggests that the nest attracts micro-organisms required as food by the fry and prevents the young from being carried away by floods. He also believes that the mouthing of the eggs and fry as they are returned to the nest protects them from bacterial damage as demonstrated by Shaw & Aronson (1954) for the oral incubator, *Tilapia macrocephala*.

With regard to the male the nest is reported to identify the centre of his territory (Lissmann, 1932, Forselius, *op. cit.*). In this way it may have significance not only for the male that built it but for intruder males as well. It has been reported by Forselius that a male will sometimes take over the nest of another and the surrounding territory along with it. He also reports that a nesting male is more aggressive than at any other period and hence better able to maintain his territory. This has obvious adaptive significance for the mating that is to follow. Whether or not the presence of the nest causes the increased aggressiveness is not clear, but during the nest-building period and the nurture period aggressiveness is reduced. The male reacts to the nest by attempting to lead the female under it and rarely, if ever, mates with her at any other place. This serves to concentrate the eggs in a relatively small area at the time of their release and makes it less likely that many of them will be lost.

It is also possible that a nest releases certain behavioural patterns in the female. Thus Forselius reports (*op. cit.*) that a roving, sexually ready female identifies the male's territory by the presence of the nest and is thus stimulated to enter it. Thus the nest has for her the significance of establishing the presence of a sexually ready male. Our own observations confirm this; for we have often observed a positive reaction to a nest when the male had been removed from the aquarium. It has also been reported by Smith (1945) and Forselius (*op. cit.*) that during spawning the females assist the males in placing eggs in the nest. As has been previously stated we have never observed this activity on the part of the females. Its absence may be a peculiarity of our breeding stock or the testing situations may have been different. The absence of female participation occurred under a wide variety of conditions, however. Neither of the authors just cited mentioned whether such behaviour was characteristic of the females or rare. If the assumption is made that this is the characteristic behaviour of mating females, one must conclude that the nest has for them the same significance that it has for mating males.

All of the above has concerned nests built by males. The significance of bubble-making and the production of small nests by the females still requires clarification. It seems certain that nesting behaviour by the females immediately prior to mating would disrupt the mating process. It is not part of the regular mating ritual and should cause the male to react to the female as an intruding male. While most male anabantids exhibit reduced aggressiveness during the nurturing period, this is by no means generally true of male *B. splendens*. Any interference with the nest by the female at this period produces an attack. Thus it is difficult to understand how female nesting can have any adaptive significance for the species. The facts cited are all in agreement with the observations of Smith, Forselius, and Lissmann in the works previously cited. It seems reasonable to suppose that nesting behaviour in the females is roughly comparable to the presence of nipples in male mammals i.e. a behavioural pattern that is present in both sexes but with adaptive significance only for one.

Forselius (*op. cit.*) emphasises the high order of individual variability of anabantid behaviour. One of the most striking characteristics of nesting activity in both sexes was the variability of its forms of expression. This was particularly true with regard to the age at which the first nest bubbles appeared. Among the males the first bubbles appeared as early as 53 days and as late as 290 days, while among females the comparable spread was from 81 to 346 days. This would suggest that the onset of full sexual maturity also

varies widely among individuals. This is consistent with our experience in breeding Siamese Fighting Fish. Successful matings have occurred when both participants were as young as 96 days, while other individuals have failed to breed until they were a great deal older. Since the bubble-blowing activity of the males begins earlier than that of the females, it is suggested that persons attempting to breed young *B. splendens* might have better success if they mated the younger males with somewhat older females.

Nesting activity increased in both sexes as the individuals grew older. Not only did more individuals participate but also those that had already demonstrated their nesting ability spent more of their available time making bubbles. Here again a striking fact is the amount of variability present. Also, it would appear that once an individual begins to produce bubbles, regardless of the age at which this occurs, it tends to increase the amount of time spent in this activity as time passes. On this basis certain individuals may be considered as still young or immature at an age when certain of their litter mates are mature or "middle-aged." This is consistent with the thinking of those investigators who suspect that growth and aging among fish involves factors other than those which pertain to other vertebrates. Furthermore, if the production of nest bubbles is considered as evidence of sexual maturity, the males may be considered as developing more rapidly than the females in that respect. This acceleration of male development would have adaptive significance for the species, since the greater part of the mating and nurturing responsibility devolves upon them. In line with this apparent tendency for the males to be favoured with regard to the time of the onset of sexual maturity and the acceleration of the development of nesting activity is the fact that they are able to mate with greater frequency than the females (Goodrich & Taylor, 1933; Forselius, 1957). Also, young males tend to be small and yet are able to mate with females larger than themselves. On the other hand, young, and consequently small, females produce few eggs when they are able to produce any at all. Thus it would appear to be advantageous for the species to have the females delay their attainment of full sexual maturity until they have reached a size that enables them to produce a sufficient number of eggs to insure the survival of adequate numbers of young. All of the above suggests that the differences with regard to the time of onset and acceleration of development of nesting activity when males are compared with females fit in well with the requirements of the species.

When the sizes of the nests built by members of the two sexes are compared, the advantage clearly lies with the males. They alone built nests of size adequate to have practical value for the nurture of the young. Again this is consistent with our observation that mated females take no active part in the nesting procedure. Forselius (*op. cit.*) suggested that the maximum size of nests built by a particular individual anabantid in terms of the number of bubbles is consistent and that in *Colisa lalia* there is correlation between the size of the nest and the size of its producer. Under the conditions of our study this was not observed for *B. splendens*.

Forselius also indicated that the shape of the nests built by the various anabantid species is the result of genetic as well as environmental factors. The observations reported here gave no evidence of any consistency in shape. This may have been due to the strong influence of the shape of the fish containers, which were small and circular. Nests have been observed in large aquaria, however, and there they also exhibit great variability of shape. When possible, the fish will build under a broad leaf or artificial substitute and adapt the shape of the nest to that.

There was a decided increase in the proportion of effective nests built by bubble-producing males up to 150 days of age. This indicates that during the age period of 53-150 days, the older males are more apt to build the larger nests. Again, variability enters the picture since a few males built adequately before they were 66 days old, while others did not do so until they had passed 276 days. Caution is indicated in interpreting these data, however, since it is possible that certain of the bubble-producers that did not build adequate nests would have done so in the presence of sexually ready females or other outside influences. Thus the actual percentages given in Table VI may have little significance, although the tendency for older individuals to produce more effective nests up to 150 days still holds good.

A great deal of work still remains to be done with regard to the effects of outside influences upon the frequency of nesting activity. Goodrich & Taylor (1934) reported that temperature had a determining effect upon the mating activity of the males as measured by nest-building and the spawning interval of the females. Forselius (*op. cit.*) suggests without the presentation of quantitative evidence that visual stimulation, meteor-

ological conditions, presence or absence of neighbours in the same container, and presence or absence of neighbours that can be seen without actual contact all are important in the case of *Colisa lalia*. He also indicates his belief in a cyclic aspect due to internal factors.

These observations have served to indicate that males, at least when they are young, will produce bubbles even when visually isolated and also that both sexes will do so under all possible permutations of one or two neighbours visible to them but not in actual physical contact.

Summary

1. Considered as a group the males began nesting earlier than the females and accelerated at a more rapid pace. This accounted for some, but not all, of the difference between them with regard to nesting activity during the developmental period.

2. The increased nesting activity noted for both sexes as the groups grew older was in part due to increased activity of the nesting fish; i.e. it was not entirely the result of the addition of more nesting individuals.

3. Male nesting activity exhibited greater acceleration during the first and last stages of the developmental period, while female nesting increased gradually throughout.

4. Participation in nesting activity became almost universal by the end of the developmental period. This was true for both sexes.

5. Most nests lasted five days or less, regardless of the sex of their builders.

6. No correlation was discovered between nest duration and the age or sex of the individuals which built the nests. Also there was no evidence that particular individuals tended to build nests of short duration or vice versa.

7. Only the males demonstrated the ability to build nests of a size adequate for the successful nurture of the young.

8. During days 53-150 age appeared to be a factor in the construction of effective nests by the males. Thereafter age had no apparent influence.

9. No evidence was uncovered to indicate that isolation or the presence of neighbours of either sex effected the frequency of nesting activity.

REFERENCES

Braddock, J. C. & Braddock, Z. I. (1955). Aggressive behaviour among females of the Siamese Fighting Fish, *Betta splendens*. *Physiol. Zool.*, **28**, 152-172.

Forselius, Sten (1957). Studies of anabantid fishes. *Zoologiska Bidrag fran Uppsala,*. **32**, 93-599.

Goodrich, H. B. & Taylor, H. C. (1934). Breeding reactions in *Betta splendens*. *Copeia.*, **4**, 165-166.

Lissmann, H. W. (1932). Die Umwelt des Kampffischen (*Betta splendens* Regan). *Z. vergl. Physiol.*, **18** (1), 65-111.

Regan, C. T. (1909). The asiatic fishes of the family Anabantidae. *Proc. Zool. Soc. Lond.*, 767-787.

Shaw, E. S. & Aronson, L. R. (1954). Oral incubation in *Tilapia macrocephala*. *Bull. Amer. Mus. nat. Hist.*, **103** (5), 375-416.

Smith, H. M. (1937). The fighting fish of Siam. *Nat. Hist.*, **39**, 265-71.

Smith, H. M. (1945). The fresh-water fishes of Siam or Thailand. *U.S. Nat. Mus. Bull.*, **188**, 456-461.

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THE "SHAKING" OF WORKER HONEYBEES BY OTHER WORKERS

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Introduction

It is now becoming realised that there are likely to be several systems of communication between members of a colony of honeybees (*Apis mellifera* L.). The two best known are (1) the fanning and scenting of homecoming bees at the hive entrance (Sladen, 1901; Ribbands & Spiers, 1953), and (2) the recruiting dances which give information about the location of nectar and pollen sources (von Frisch, 1946) and sites of new homes (Lindauer, 1951). In addition, the piping both of old queens (Allen, 1956; Woods, 1956) and of virgins at swarming time is presumably not without significance to the colony, and may probably be included under this heading.

There are other events within the hive that one might expect to be initiated by special forms of communication, including the departure of swarms, the mobilisation of the colony when intruders enter the hive and possibly the commencement of foraging each day, but up to the present they have not been shown to be preceded by any special type of behaviour. There are also activities which have interested several observers because of a resemblance to recruiting dances, but for which no satisfactory interpretation has yet been put forward. These activities are characterised by a quivering movement of the body which is somewhat similar to the waggle run of a recruiting dance, but no regular pattern of progress on the comb, such as a round or a sickle movement, has been detected. Two main classes of behaviour of this type have been described. In the first, the quivering movements of the body are either irregular or from side to side and no definite contact is made with other bees (shiver dances and grooming dances); in the second the body vibrates dorsoventrally and regular contact is made with other bees (shaking).

Up to the present more attention has been paid to the first type of behaviour than to the second, shiver dances being described by von Frisch (1923), Lindauer (1948), Schneider (1949) and Schick (1953), and the grooming dance by Haydak (1945) and Milum (1947). During the course of the present observations the descriptions of these earlier workers have in general been verified. The "grooming dance" seemed to be an involuntary series of movements very possibly caused by the presence of debris on the thorax and it often, but not always, resulted in another bee cleaning the dorsal side of the thorax, after which the so-called dance nearly always ceased. Shivering also appeared to consist of movements at random on the comb, but differed from the grooming dance in sometimes continuing for relatively long periods without cessation, apparently eliciting no response from the neighbouring bees.

The same continuous activity was often observable during shaking, which has been described in detail by Schick (1953). He states that one bee would go up to a succession of others and, while holding each one in turn either with its forelegs or with all three pairs of legs, would shake its body very rapidly. This shaking started with a quick vertical movement of the abdomen, rapidly extending to the rest of the body. At times a bee might shake on an empty comb, but normally the main differences from the shiver dance and the grooming dance lay in the regular contact made with other bees. Both old and young bees were shaken and during the shaking they remained still (even if they had previously been doing a shiver dance), taking up their previous occupations again after it had finished.

Schick gives details of observations on shaking which were made during experiments upon the effect on bees of urethane and nipasol and he states in his summary that it can often be seen under normal conditions. Although he concludes that shaking could be caused by urethane and sometimes by nipasol, he does not mention whether any assessment was made of the amount of shaking occurring before the feeding of these two substances commenced. Further, in an experiment where only a limited number of bees were trained to a feeding dish, he observed that in addition to 10 out of 12 of these marked foragers which were seen to shake, there were also 23 unmarked bees shaking during the same period. He assumed that these unmarked bees were "house" bees which had received nectar from the incoming marked foragers, but he does not appear to have considered the fact that they

might have been foragers from another, uncontaminated, site.

Istomina - Tsvetkova (1953) also observed workers shaking one another and recorded that on one occasion a bee shook 84 others in succession. Although she did not discover the stimulus causing the onset of shaking she believed that the process might be connected in some way with mobilisation for flight.

Haydak (1945) believed that shaking occurred when hive conditions were at an optimum, such as during a honey flow, but Milum (1955) stated that shaking was seen "at all hours of day and night, in winter and in summer, with and without flight, and even in queenless colonies and in colonies at the point of starvation." He therefore disagreed with Haydak's conclusion, but quoted few actual results in support of these statements. He did not record any workers less than nine days old shaking other workers and reported that some of the shakers were old bees.

Not only workers but also queens may be shaken and the results of work on queens by the present writer have already been published (Allen, 1958, and 1959). It was found that the frequency of shaking rose to a peak at swarming time, and the conclusion from this and other evidence was that its function was connected with the departure of the queen from the hive. The act of shaking appears to be the same whether it is the queens or workers which are shaken, and in both cases its apparently purposeful and regular nature contrasts markedly with the grooming and shivering dances. It might be expected from this similarity between the process in queens and workers that its function would be related in the two castes, and in order to investigate this matter the work described in the present paper was undertaken.

Details of Experimental Colonies

Three colonies were used: Colony B (May-July 1955, Colony C (October 1956-December 1957), and Colony D (April-August 1958). Each was housed in an observation hive containing either three or four British Standard brood combs and the bees could fly freely at all times. A heating unit controlled at a nominal 27°C. at the thermostat was in operation in the hives throughout the observations on Colonies C & D.

The approximate number of bees in Colonies B & C have been given in an earlier paper (Allen, 1959), and details of Colony D (1958) follow:

22nd April:	3,700 bees
6th June:	4,800 bees
28th June:	10,000 bees
29th July:	8,400 bees
4th August:	5,500 bees

Swarm preparations were made in this colony as in the others and the prime swarm departed on 25th June. Many of the swarm bees returned to the hive during the next few days, however, and consequently the number of bees was not greatly diminished.

In Colonies B and C groups of newly-emerged bees were marked twice weekly with spots of paint of a different colour for each marking day, giving populations containing bees of known age. Further details are given by Allen (1959).

Results

(1) Counts of Numbers of Bees Shaking at Different Times

Shaking was observed in winter as well as summer but was noticeably more frequent during the summer months. During the winter in particular it seemed that it occurred only at times when the bees were flying, and in order to discover whether there was a general correlation with flight activity throughout the year counts of the numbers of shakers and of the number flying from the hive per minute were made on Colony C between 24th October 1956, and 15th December 1957. In order to facilitate counts of the numbers of bees shaking, parallel vertical lines 1¼ in. apart were marked on the glass windows of the hive. Next, to ensure that comparable counts could be made at varying colony sizes the boundaries of an area of comb covered by approximately 2,000 bees were decided upon at the beginning of each count; then, starting at one side of this area, the bees within each pair of lines were scanned in turn, and the number of shakers recorded. The rate of scanning was such that each complete count of the area had a duration of approximately 60 seconds, so that each bee observed during different counts received the same amount of attention, and there was thus an equal probability of recording any shaker present.

A total of 90 groups of counts (each consisting of five consecutive counts) were made at various times during the hours of daylight (most often between 9 a.m. and 3 p.m. G.M.T.), and the results are presented in Fig. 1 in the form of the mean values per count for the first and second halves of each month respectively. It is evident that the incidence of shaking was markedly increased in the summer as compared with the winter.

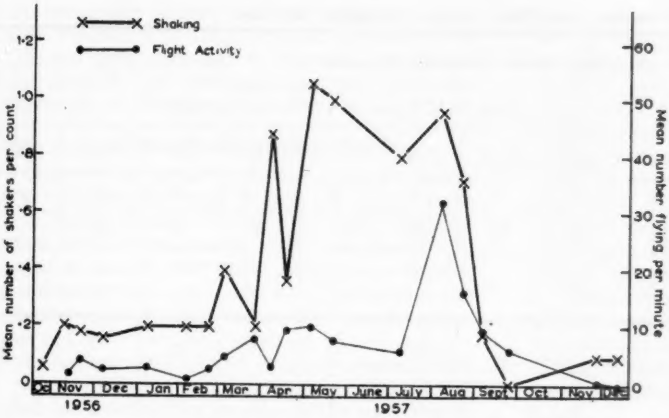

Fig. 1. Annual incidence of shaking (½-monthly means).

Flight activity was estimated by counting the number of bees flying from the exit of the hive per minute, either immediately before or immediately after the counts of shaking, between 13th November 1956, and 15th December 1958 (81 counts). It followed a course which was broadly similar to that of shaking (except that it showed a marked peak in August), having higher values in summer than in winter, as Fig. 1 shows. However, this fact in itself is insufficient to prove a direct relationship between the two activities, since other factors—for example, the quantity of brood in the colony (Nolan, 1925; Allen & Jeffree, 1956)—also have rather similar cycles.

The daily incidence of shaking was the next point to be investigated and for this purpose Colony D was studied. The same techniques for estimating the amount of shaking and flight activity were used as in Colony C, except that the whole colony was scanned for shakers, in place of the 2,000 bees scanned in Colony C. In order to standardise the new technique the number of bees in the hive was estimated just prior to making every group of five counts and the duration of each count was adjusted so that approximately 2,000 bees were scanned per minute. The method of estimating the total number of bees present was to compare both sides of each of the three combs with a set of carefully calibrated photographs (Jeffree, 1951) and to sum the results. Counts were made at intervals of 1¾ hours from dawn to dusk on dates between 25th April and 4th June. On certain of these dates the set of observations was divided into two separate periods, one extending from dawn until 10.15 a.m. on one day and the other from noon until dusk on either the preceding or succeeding day. Altogether, six complete daily records were obtained covering late April to early May and late May to early June (Table I). In the first period recordings were made between 5.00 a.m. and 7.00 p.m. G.M.T. (except on 30th April when there were additional counts), while in the second period two extra counts at 3.15 a.m. and 8.45 p.m. were included to cover the increased length of day. Fig. 2 shows that curve of the overall mean values throughout the day rose from zero at 3.15 a.m. to a fairly steady level during most of the daylight hours and then again fell to zero by 8.45 p.m. It seemed clear from the results that shaking normally commenced after daybreak and ceased before darkness fell in the evening.

The position with regard to flight activity was that there were resemblances between the fluctuations in the levels of the two activities but that these were not sufficiently consistent to suggest a direct relationship. It did, however, seem that shaking commenced each day before any flights were made and normally continued for a time after flying had ceased for the day (Table 1 and Fig. 2) but no other conclusions could be reached. In general, bad weather conditions tended to be associated with a reduction in the incidence of shaking; no clear correlations could be obtained between the number shaking at any one time and the temperature, barometric pressure, wind speed and sunshine, although temperature showed some indications of having a slightly greater effect than the other factors.

(2) Ages of Bees Concerned in Shaking

The most satisfactory method of investigating the frequencies with which bees of different ages were engaged in shaking was obviously to record each relevant occasion when a marked bee was observed to shake ("*direct count*"), but while this ideal technique could be employed without difficulty for clearly finite activities where the event studied was of short duration (e.g. the number of bees of different ages shaken) it was less simple in the case of the shakers themselves, since one bee might shake others almost continuously over

Table I. Shaking and Flight Activity Throughout the Day.

Date	3.15	5.00	6.45	8.30	10.15	12.00	1.45	3.30	5.15	7.00	8.45
A. Mean number of shakers per count.											
	a.m.					Time (G.M.T.).			p.m.		
25th April	(o)*	4	4	0	1	1	0	0	0	0	—
30th April	—	19	22	42	26	25	10	8	1	2	—
7th May 8th May	—	8	5	5	4	0	8	1	1	0	—
21st May 22nd May	0	28	50	46	36	17	65	17	14	2	0
26th May 27th May	0	13	14	13	24	32	34	18	17	7	0
3rd June 4th June	0	3	6	10	6	9	15	17	12	9	0
B. Mean number of flights per minute.											
25th April	(o)*	0	1	37	0	0	0	0	0	0	—
30th April	—	1	25	16	22	3	10	1	0	0	—
7th May 8th May	—	1	2	0	1	1	0	0	0	0	—
21st May 22nd May	0	0	56	49	32	8	42	49	2	0	0
26th May 27th May	0	2	1	0	62	15	45	14	0	0	0
3rd June 4th June	0	0	1	0	1	70	15	37	2	1	0

* Count made at 4.30 a.m.

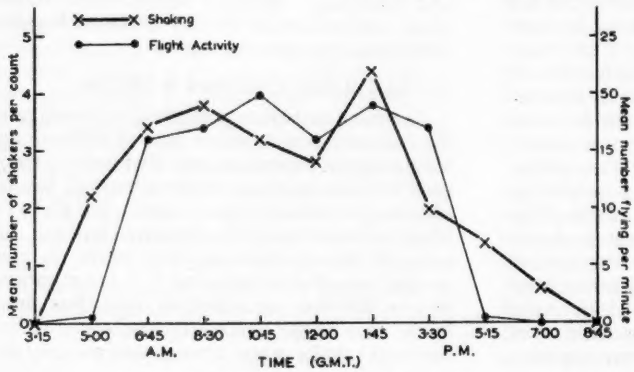

Fig. 2. Daily incidence of shaking.

a period of many minutes, and unless it was individually marked it could have been confused with other marked shakers of the same age (which would have had marks of the same colour). Bees were given individual marks in Colony C in 1957, but the numbers which could be so marked were limited and too few were observed in the act of shaking to give reliable results.

An alternative method to that of the direct count was to record the first shaker of each age-group observed each day, and this "*group method*" was adopted to determine

the age ranges of bees involved and also to give some indication of frequencies of appearance of different ages, although it was appreciated that this method had limitations and that care was needed in the interpretation of the results.

(2a) Ages of Shakers and of Bees Shaken

Only the records from the dates on which marked bees of at least 35 days old were present in Colonies B and C (31st May 1955, and 2nd May 1957, respectively) were considered, in order to ensure that there were proportionate numbers of all ages in the hive throughout the observations. In both colonies observations on marked bees were discontinued after the prime swarms departed (7th and 13th July, respectively)

As mentioned above, the "group method" was used for determining the ages of the bees seen to shake others, and Fig. 3 gives the results for the two colonies. The two distributions are very similar and the overall age range was 2-61 days. The apparent peak occurred at about the fourth week in Colony B and between the fourth and fifth weeks in Colony C, but owing to the effect of the "group method" on the relative numbers of each age recorded the peak is almost certainly reduced in height and extended in duration in relation to the true age distribution, as the following explanation will show. Since only the first bee belonging to each colour (age) group observed on any one day was recorded, it is clear that a group represented on several occasions that day will have carried no more weight in the records than a group represented only once. At the lowest levels of the curve bees of a single colour group were seldom seen more than once, and so the curve was only slightly distorted; but at the highest levels it was very frequently the case that more than one bee of a group was observed, yet that colour group still received only one record. This had the effect of flattening out and extending the peak of the curve, and also possibly of somewhat altering its centre.

The ages of marked bees shaken by marked shakers in Colony B were also recorded, and here the method of a direct count could be employed since, when considering the recipient, the process was of only a few seconds duration. The results are given in Fig. 4 and they show a peak situated approximately in the second and third weeks of adult life, and an age-range of 0-55 days.

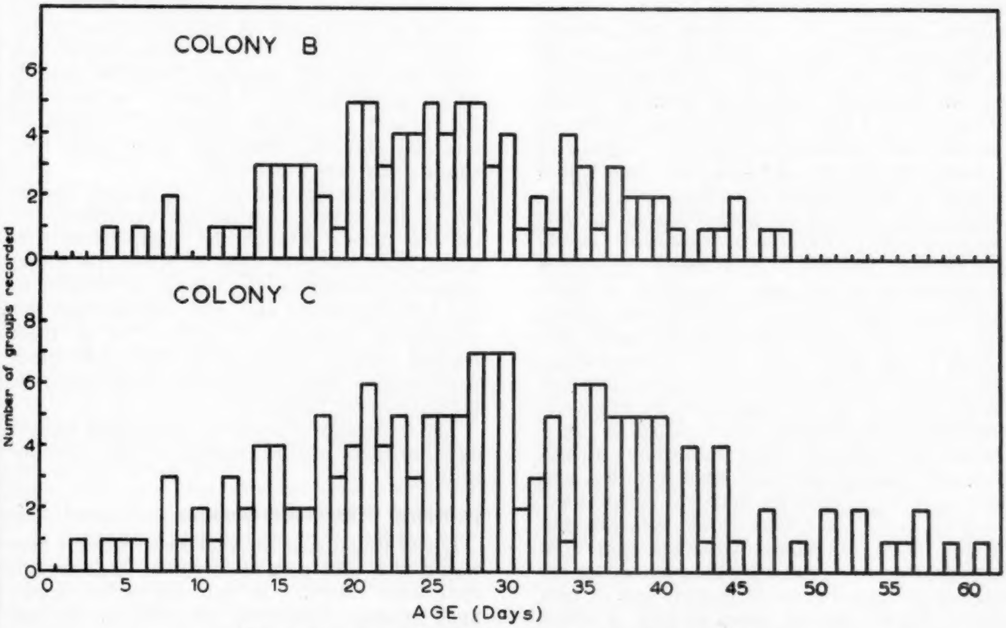

Fig. 3. Ages of workers shaking other workers (group method).

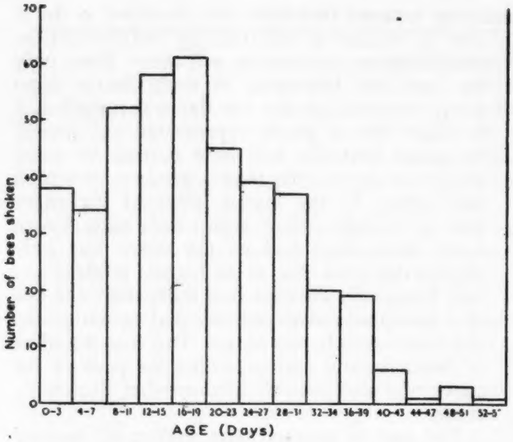

Fig. 4. Ages of bees shaken (direct count).

These results on the ages both of the shakers and of the workers shaken show a very similar age range covering the entire life span of the bee. However, the relative proportions of bees of each age concerned with shaking are of more interest than the actual age range, for these figures represent the general trends of behaviour in the colony, whereas the age range may include results from individuals exhibiting some atypical or only sporadic behaviour. Such proportions are not immediately apparent from the results given in Figs. 3 and 4 unless the total number of marked bees remained constant at all ages, and it must logically be supposed that there would be a fall in the numbers of *marked* bees with increasing age because the probability of any one bee having died is likely to increase progressively day by day, resulting in a declining population of marked bees with age. The effects of these declining populations in the different age groups cannot be said to have distorted the results presented in this paper since they correspond approximately with the natural condition, but they must be taken into consideration in any interpretation of the findings. For example, in Fig. 4 the numbers and not direct proportions of bees shaken at various ages have been recorded, and here (as in Fig. 3 also) the apparent decline after the peak in the third week would coincide with the fall in total numbers of marked bees. It is possible, therefore, that after the peak values are reached the proportions of shakers and of bees shaken did not decline again as Figs. 3 and 4 apparently indicate, since these declines could simply have been the direct result of the decline with age in the total numbers of marked bees. In contrast, the rise to the peaks in both Fig. 3 and Fig. 4 is contrary to this trend, which would strongly suggest that in proportion to the total numbers of marked bees of the appropriate age present in the colony few of the young bees shake others or are shaken themselves, and that the proportion rises as they become older.

The relationship between the ages of the shakers and the ages of the bees shaken was investigated but there was no evidence of any correlation. Neither did it seem that individual shakers tended to shake a particular age-range of workers.

(2b) Frequency of Shaking by Individual Bees

The frequency with which any one bee shook others varied very greatly. In some cases the shaker passed directly from one bee to an adjacent one with great regularity (for a period of at least ten minutes and probably very much longer), while in other cases the shaker moved slowly over the comb and shook only a few bees. The position was further complicated by certain shakers which paused for several minutes between periods of relatively rapid shaking. In order to ascertain whether these differences were related to differences in age, in Colony B between 16th May and 16th July 46 marked shakers were each watched without a break for periods which varied between 1 minute 5 seconds and 25 minutes 25 seconds (mean=5 minutes 35 seconds) and the frequency with which they shook other bees was noted.

The frequencies are plotted against age in Fig. 5 and have a considerable variability, but the line drawn through the mean values (obtained from groups of eight, or in one case seven, points at consecutive ages) shows a tendency to rise with increasing age. This increase was not statistically significant ($P<0{\cdot}1$). Five of these marked shakers shook more than 100 other workers while under continuous observation, the highest number being 175.

The frequency of shaking was plotted against date but there was no evidence of any relationship.

Individual Behaviour of Shakers

It was found that the shakers of worker bees would also take part in foraging, since certain ones were recorded as carrying pollen loads. Such shakers frequently interspersed shaking with dancing, making a few waggle runs and

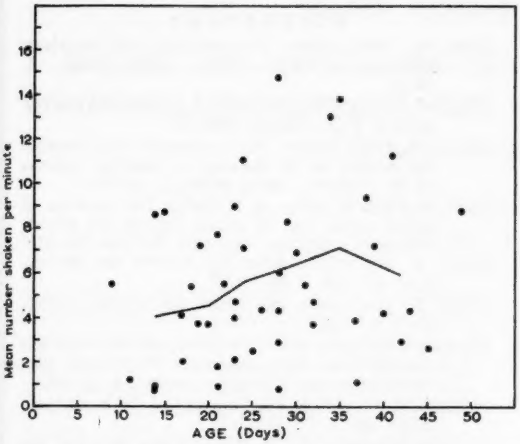

Fig. 5. Frequency of shaking related to age of shaker.

then shaking again. The runs tended to be somewhat hesitant and at times rather erratic when alternating with shaking, but individual behaviour varied considerably. For example, a 49-day old bee did not remove its pollen loads until $6\frac{1}{2}$ minutes after it was first observed, during which time it shook 59 workers. It then shook another 23 workers and made two separate short and hesitant waggle runs between periods of shaking before being lost to sight near the exit of the hive. On another occasion when a marked bee designated as Y^1 was watched for the first time it was seen to follow a dancer and then continue shaking as before. Later, however, Y^1 itself had pollen loads and was making slow waggle runs followed by irregular movements over the comb. After removing the pollen loads it remained in the hive for 2 minutes 20 seconds, shaking other bees vigorously and also making a few more waggle runs before flying again. During the following morning it was still shaking and although it came into close proximity with 4 dancers in the course of $8\frac{1}{2}$ minutes it showed no interest in them, although it made a single waggle run during this period. $3\frac{1}{2}$ hours later its shaking was interspersed with dancing, with the direction of the dance constant except on two occasions. Two days later it was shaking normally even though foragers were bringing in pollen.

In a few cases a shaker probably left the hive after following a dancer but on more occasions it continued shaking. At times there were signs of a definite avoidance of the dancers.

There is little information as regards the length of the period over which a bee continues shaking, but individually marked bees have been recorded as shaking at different times on the same day, and four individuals were recorded on different days. One of these was shaking on two consecutive days, two (including Y^1 mentioned above) over periods of four days, and one over a period of fourteen days.

Activities of Workers After Being Shaken

Twenty marked workers in Colony B were watched for periods ranging from one to twelve minutes (mean duration=5 minutes 5 seconds) after they had been shaken, but they showed no tendency to engage in any one type of activity. Two of these bees were themselves shakers, and resumed shaking almost immediately afterwards.

Discussion

The results on the ages of shakers of worker bees agree with those found for the shakers of the queen (Allen, 1959), which ranged from 3 to 61 days, with the highest proportions shaking in their fourth week of life. In the present observations increasing proportions of workers shook other workers during approximately the first three weeks of adult life, and thereafter there was probably little change. The shakers apparently moved from one worker to another quite randomly, but analysis of the results showed that they tended to shake the youngest bees relatively less often than those of about two weeks old or over. It seems, therefore, that the youngest bees neither shook nor were shaken with as great a frequency as the older bees.

The incidence of shaking among the workers proved to be higher in summer than in winter, whereas queens are only shaken to any extent at the time of their mating and swarming flights (Hammann, 1957; Allen, 1959). For example, in Colony C the shaking of the workers had a quite appreciable incidence during April and May (Fig. 1), while in the same colony the queen was barely shaken at all until late June (Allen, 1959). The two findings are, however, not necessarily in conflict if the hypothesis that the shaking of queens is connected with their flights from the hive is correct (Hammann, 1957; Allen, 1959), since the queens only leave the hive at the mating and swarming seasons, while the workers do so on any day of the year when conditions are suitable. The fact that the shaking of workers apparently occurred only during the hours of daylight also conformed to the view that there was a connection with flight activity, but in spite

of a similarity between the fluctuations in the levels of shaking and flight activity the agreement was not sufficiently close to postulate a direct relationship.

The shaking of the workers may be a more complicated process than that of the queens, and so far it has not been possible to show a direct correlation between it and any other single factor. It is possible that it may have a complex relationship with a number of factors, such as weather conditions and events inside the hive.

Summary

1. Various types of distinctive quivering movements by worker honeybees inside the hive have been observed, and a detailed study of one of these ("shaking") was undertaken.

2. The workers were found to be shaken throughout the year, although with greatly increased frequency in the summer.

3. A daily cycle of shaking, commencing at daybreak and finishing at dusk, has been demonstrated. Shaking was recorded prior to the first flights of the day. Resemblances to fluctuations in flight activity could be traced but these were not sufficiently consistent to indicate a direct relationship between the two activities, nor was it possible to show a relationship with meteorological factors.

4. The ages of workers engaged in shaking ranged from 2 to 61 days, with a progressive increase in numbers up to about 3 weeks of age. Following this it is thought that there was little change in the proportion shaking relative to the total number of older marked bees in the hive.

5. There were indications that the frequency of shaking increased slightly with increasing age, but the increase was not statistically significant.

6. Workers with an age-range of 0-55 days were shaken, but the younger bees were shaken less frequently than the older.

7. The behaviour of individual shakers and of bees shaken is discussed briefly.

REFERENCES

Allen, M. Delia (1956). The behaviour of honeybees preparing to swarm. *Brit. J. anim. Behav.*, **4**, 14-22.

Allen, M. Delia (1958). The shaking of honeybee queens prior to flight. *Nature*, **181**, 68.

Allen, M. Delia (1959). The occurrence and possible significance of the shaking of honeybee queens by the workers. *J. anim. Behav.*, **7**, 66-69.

Allen, M. Delia & Jeffree, E. P. (1956). The influence of stored pollen and of colony size on the brood-rearing of honeybees. *Ann. appl. Biol.*, **44**, 649-655.

Frisch, K. von (1923). Über die Sprache der Bienen. *Zool. Jb.*, Abt. 3, **40**, 1-186.

Frisch, K. von (1946). Die Tänze der Bienen. *Osterr. Zool.*, **1**, 1-48.

Hammann, Eleonore (1957). Wer hat die Initiative bei den Ausflügen der Jungkönigin, die Königin oder der Arbeitsbienen? *Insectes sociaux*, **4**, 91-105.

Haydak, M. H. (1945). The language of the honeybees. *Amer. Bee J.*, **85**, 316-317.

Istomina-Tsvetkova, K. P. (1953). (New data on the behaviour of bees). *Pchelovodstvo*, (9), 15-23.

Jeffree, E. P. (1951). A photographic presentation of estimated numbers of honeybees (*Apis mellifera* L.) on combs in 14 × 8½ inch frames. *Bee World*, **32**, 82-91.

Lindauer, M. (1948). Einwirkung von Duft und Geschmacksstoffen auf die Tänze der Bienen. *Z. vergl. Physiol.*, **31**, 348-412.

Lindauer, M. (1951). Bienentänze in der Schwaumtraube. *Naturwiss.*, **38**, 509-513.

Milum, V. G. (1947). Grooming dance and associated activities of the honeybee colony. *Illinois Acad. Sci. Trans.*, **40**, 194-196.

Milum, V. G. (1955). Honeybee communication. *Amer. Bee J.*, **95**, 97-104.

Nolan, W. J. (1925). The brood-rearing cycle of the honeybee. *Bull. U.S. Dep. Agric.* No. **1349**, 1-56.

Ribbands, C. R. & Speirs, Nancy (1953). The adaptability of the home-coming honeybee. *Brit. J. anim. Behav.*, **1**, 59-66.

Schick, W. (1953). Über die Wirkung von Giftstoffen auf die Tänze der Bienen. *Z. vergl. Physiol.*, **35**, 105-128.

Schneider, F. (1949). Über die Vergiftung der Bienen mit Dinitrokresol. *Schweiz. entomol. Gesells.*, **22**, 294-308.

Sladen, F. W. L. (1901). A scent-producing organ in the abdomen of the bee. *Glean. Bee Cult.*, **29**, 639-40.

Woods, E. F. (1956). Queen piping. *Bee World*, **37**, 185-195, 216-219.

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BRIEF COMMUNICATIONS

ESCAPE AND AVOIDANCE LEARNING AS A FUNCTION OF EMOTIONALITY LEVEL IN THE WYOMING GROUND SQUIRREL *Citellus richardsonii elegans*

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The object of this study is to determine whether a significant difference might exist in the learning of escape and avoidance from electrical shock between thoroughly cage-conditioned and freshly caught Wyoming ground squirrels. The problem suggested itself following the reading of Spence's (1956) *Behaviour theory and conditioning*, Miller's (1948) *Fear as an acquirable drive*, and certain observations of wild animal behaviour in both field (1959-1956) and laboratory (1957 a & b). The concensus seems to be that anxious subjects (human) condition faster and to a significantly higher level than less anxious subjects. Rather different hypothetical constructs have been utilised in attempts to throw light on the situation, notably by Spence & Taylor (1953), Hilgard, *et al* (1951) and Miller (*op. cit.*). Having at hand a group of newly-caught and apparently "emotional" ground squirrels and a standard stock of well cage-conditioned squirrels of the same species, we felt that data obtainable from them might throw some further light on the general problem of learning an instrumental response by emotional and less emotional subjects.

Method

Thirty-six adult male Wyoming ground squirrels were the subjects in these experiments. They were captured by the author from the same area of approximately a square mile near Laramie, Wyoming. Members of one group were captured no more than ten days before the beginning of the experimental work. This group was labelled "New". Its members showed many signs of "wildness" or "anxiety", such as high defecatory, urinary, and vocalisation rates and frequency, both in and out of the immediate presence of the observer. These also reacted much more violently to handling than did the cage-conditioned group. Members of the second group had been confined to the laboratory colony for at least a year. These animals were much lower in anxiety-associated responses of the type cited above. This group was labelled "Old". Animals of both groups were mature and comparable in weights.

Although the author had had fifteen years' experience working with ground squirrels in the laboratory and felt that he knew that newly caught subjects were significantly more "emotional" than those adequately cage-conditioned, he had never run actual emotionality scores until undertaking the present series of experiments. Subjects were observed in their home cages in a series of five-minute check periods on successive days. A clean paper was introduced into the dropping tray at the beginning of each observation for fecal pellet counts and urination determination. If a subject vocalised in three of the five minutes, a positive score was recorded for this criterion.

The conditioning apparatus was a standard shocking grid 50 cm. × 30 cm., either half of which could be activated by an induced current to serve as the unconditioned stimulus (US). The conditioned stimulus (CS) was a 60-cycle buzzer. The grid covered the floor of a cage 30 cm. high, the two halves being separated by a fence 15 cm. high. The subjects were visible to E through a suitably illuminated one-way vision mirror.

All subjects were allowed to explore the conditioning apparatus for ten minutes on each of three days with buzzer and shock off, and were then given three sessions each of 3S. Sixteen subjects which persisted in responding to the CS by jumping the fence were eliminated from the experiment. Two animals either died or became seriously ill and were eliminated for that reason. Eighteen subjects were now exposed to the following regimen: two minutes adjustment to apparatus, 30 seconds CS, 30 seconds US. If the subject did not cross, he was placed on the other side, and all had the procedure repeated in the opposite direction. Fourteen daily pairs of trials were made for each S. Latencies of response to CS, US, and other incidental notes were made by E.

Results

As far as defaecation, urination and vocalisation may be accepted as criteria of "emotionality", the newly caught were significantly more emotional than the cage-conditioned subjects.

Table I. "Emotionality" Scores (per animal-trial)

N		Defecation	Urination %	Vocalisation %
Old	19	5·35±2·49	17·54	50·9
New	17	10·60±2·92	37·25	84·3
	t	9·47	2·23	3·55
	p	<·001	<·05	<·001

Response to US

Although not all subjects escaped from shock on even the last trial (78 per cent.—old and 67 per cent. new, see Fig. 1), all had shown escape response to US during the series. There was no significant difference between old and new groups in incidence of escape response.

There was a significant difference in escape latencies. The new group responded much faster to US.

The new group showed a significantly lower level of learning avoidance response. On the last trial 36 per cent. of the old group responded to the CS, whereas none of the new group gave such a response. There was no significant difference in avoidance response latency between the two groups.

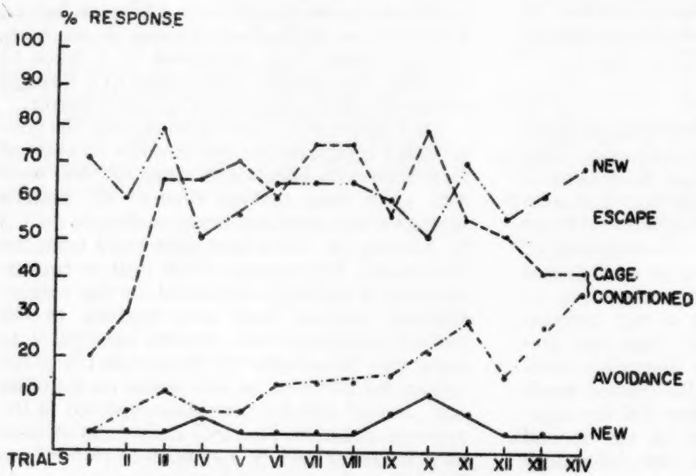

Fig. 1. Average escape and avoidance frequencies.

Table II. Escape Response

	Incidence	%	Seconds latency
Old	127/222	57·20	11·1 ± 1·38
New	156/246	63·41	5·4 ± 0·48
Difference	29	6·21	5·7
S.E.Δ		4·52	·128
P		<1·0	<·001

Table III. Avoidance Response

	Incidence	%	Seconds latency
Old	31/222	13·96	15·6
New	5/246	2·03	16·0
Difference	26	11·93±2·46	·4
P		<·002	

Discussion

Although the new group of "anxious" subjects learned to respond to the shock with much shorter latency than the old, cage-conditioned group, the new group never learned to avoid the shock by responding to the warning buzzer. The old, less "anxious" group learned this avoidance response to CS quite satisfactorily. This better learning by "less emotional" subjects is, superficially at least, contrary to a large body of data which shows "high drive" subjects to be superior learners. Many of these data are summarised in Spence (1956, *op. cit.*). However, the same volume contains several suggestions which may help to explain our findings. The curve presented by Fig. 7 (p. 173) demonstrates a lessened rate of response under higher

levels of aversive stimulation. The material included in Section 7, and especially the footnote on page 222 suggests that increased oscillation between competing responses may be expected to occur at high drive levels.

One possible reason for the difficulty in learning the avoidance response apparent in our "anxious" group was that members of this group tended to "freeze" into immobility as a response to novel environmental change. The response of freezing is obviously incompatible with avoidance response. Assuming that both the CS, or buzzer and the US, or shock were aversive, the US must further be assumed to be of such a nature, quantitatively or qualitatively, that the response tendency to it was sufficiently strong to overcome the incompatible ${}_{S}U_{R}$ of freezing. In Hullian (1952) symbolism ${}_{S}U_{R}$ signifies an unlearned stimulus-response connection, and ${}_{S}E_{R}$, a present reaction potential. So for the "anxious" group:

${}_{S}E_{R}$ (Escape) $>$ ${}_{S}U_{R}$ (Freezing) $>$ ${}_{S}E_{R}$ (Avoidance).

But for the "less anxious" group:

${}_{S}E_{R}$ (Escape) $>$ ${}_{S}E_{R}$ (Avoidance) $>$ ${}_{S}U_{R}$ (Freezing).

Although it may be true that the response tendency of an organism is in part the result of total drive level, and presumably there was a greater total drive in the anxious than the non-anxious group, the only measure we have of drive is response, and if the unlearned response tendency is incompatible with the learned response, apparently paradoxical differences in response between anxious and non-anxious groups may result. We believe it to be an over-simplification to interpret these data as over-motivation interfering with the learning of an expectancy. A superficial interpretation of these results might stop with the assumption that the newly caught group failed to learn avoidance because of giving the incompatible unlearned response of freezing. A more careful examination of the situation makes it apparent that the reason the new animals froze was because they were more anxious than the cage-conditioned subjects. In animal, and possibly in human subjects, under high anxiety there is at least one other response than avoidance possible to noxious stimuli, namely freezing. Unless this possibility is recognized chaos may result in attempting to interpret data from shock conditioning.

Summary

An attempt was made to teach recently caught "anxious" wild rodents and thoroughly cage-conditioned subjects of the same species an avoidance response to a buzzer preceding shock. The less anxious cage-conditioned group learned the response more quickly and thoroughly than the more anxious group. Possibly this difference was, in part, due to the fact that newly caught animals tend to give the incompatible response of freezing to aversive but not actively noxious stimuli.

Acknowledgments

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2. The author is indebted to Mrs. Mellee Luton-Fish for many of the observational data here reported.

REFERENCES

Denniston, R. H. (1949). Certain aspects of the development and behaviour of the Wyoming moose. *Anat. Rec.*, **105**, 137.

Denniston, R. H. (1956). The behaviour, ecology, and population dynamics of the Wyoming or Rocky Mountain moose, *Alces alces shirasi*. *Zoologica*, **41**, 105-118.

Denniston, R. H. (1957a). Notes on breeding and size of young in the Richardson ground squirrel. *J. Mammal.*, **38**, 414-416.

Denniston, R. H. (1957b). Sexual behaviour and physiology cycle in an annual breeding wild rodent. *Anat. Rec.*, **128**, 539.

Hilgard, E. R., Jones, L. W., & Kaplan, S. J. (1951). Conditioned discrimination as related to anxiety. *J. exp. Psychol.*, **42**, 94-100.

Hull, C. L. (1952). *A behaviour system.* New Haven: Yale University Press.

Miller, N. E. (1948). Studies of fear as an acquirable drive. *J. exp. Psychol.*, **38**, 89-101.

Spence, K. W. (1956). *Behaviour theory and conditioning.* New Haven: Yale University Press.

Spence, D. W. & Taylor, J. A. (1953). The relation of conditioned response strength to anxiety in normal, neurotic and psychotic subjects. *J. exp. Psychol.*, **45**, 265-272.

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A CATTLE RANGEMETER

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The problem of tracking the distances travelled by grazing cattle has exercised the minds of several workers, who have produced plotting techniques, pedometers, radio control and infrared devices none of which have been very successful or easy to use for long term work (Hammond, 1955).

However, the successful development of a device for measuring the distances travelled by sheep under varying pasture regimes (Cresswell, 1957) led to a conviction that similar methods could be applied to cattle.

Accordingly developmental work was started in New Zealand with the support of the Dairy Husbandry Department, Massey Agricultural College, and the co-operation of Mr. A. W. Davey of that Department.

Designs involving the use of a light saddle and centre shaft (Plate I) and the same saddle and side shafts were not very successful. However, these designs led quite naturally to a simple but effective apparatus which was built in Utah State University, U.S.A. This includes a strong leather harness (Plate II) to the breeching piece of which is mounted a soft steel bar almost equal in length to the leather. Two steel lugs at a centre position on this steel bar give a point of attachment for a flexible joint (Plate IIA). A metal and rubber faeces-deflector may be used (Plate Ib) but a rubber sheet attached to the harness and over the top of the breeching strap is probably more effective and decidedly simpler. The faeces deflector prevents the passage of faeces between the breeching strap and the animal.

The recording device consists of a single shaft and a wheel which is maintained in an upright position by means of balancing spring steel tines (Plate IIB). These tines are free to ride up and down with the territory but are each fastened to a spring which maintains sufficient downward pressure to bring the wheel always to a vertical position. The tines are most effective guards against posts, fences, and other vertical obstructions. The distance travelled by the wheel is recorded by means of a Lucas Cyclometer.

The single shaft is extended by a flexible spring which is nevertheless rigid enough to hold the shaft with little or no sag. This makes a very effective universal joint. The spring is attached to the lugs on the breeching band by means of a length of rubber hose. At one end the hose is firmly clamped to the spring and at the other it is drilled to carry a steel tube which fits comfortably between the breeching lugs. A pin with a snap end can be quickly inserted or removed from the breeching lugs and steel tube line-up (Plate IIA). This makes the apparatus quite convenient for dairy cow work, in that the rangemeter can be removed and replaced in a matter of seconds at milking time.

This machine is to be used by Professor Lorin E. Harris and his staff in pasture and range observations during the coming year. Independent papers will be published by this group.

Acknowledgments

It is desired to make grateful acknowledgment of the co-operation and lack of scepticism of Massey Agricultural College and Utah State University. Particular thanks are due to Professors Lorin E. Harris and John E. Butcher whose budgets supported the enterprise in its latter stages. The enthusiastic help of Mr. Emmett Devine and the staff of Utah State Maintenance Shop and Professor J. A. Bennett and his livestock husbandry staff were equally essential to the success of the development.

REFERENCES

Cresswell, E. (1957). A new technique for sheep behaviour studies. *Brit. J. anim. Behav.*, **5**, 3-119.

Hammond, J. (1955). *Progress in the physiology of farm animals.* London: Butterworths Scientific Publications, **2**, 585-602.

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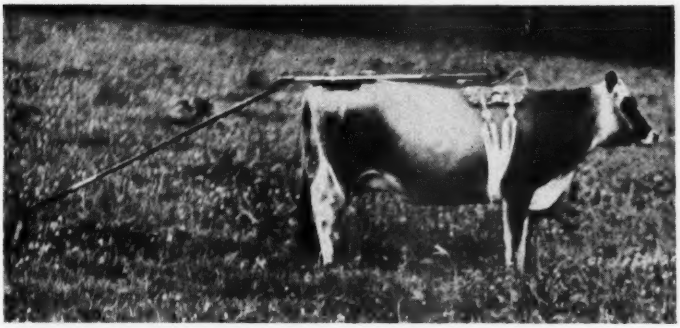
PLATE I

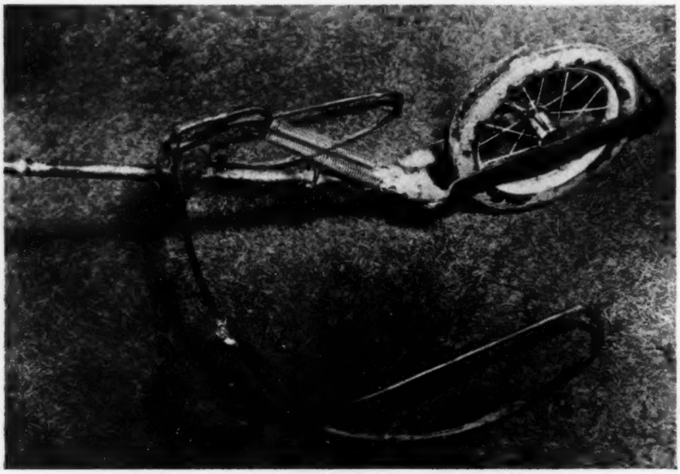


A. A preliminary stage in the evolution of a cattle rangemeter in New Zealand.

B. Cow in rangemeter harness.

PLATE II

A. Showing the mounting of the flexible joint of the cattle rangemeter.



B. The construction details of the cattle rangemeter wheel mounting.

AN ACTIVITY CAGE AND RECORDER FOR DOMESTIC FOWL*

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A number of variables is presumed to affect the motor activity of animals; however, inexpensive recording devices are not generally available to measure these effects. Three principal systems utilised for such measurement involve: (*a*) tambour-mounted cages in which movement of the cage changes the air pressure in a closed system, (*b*) spring-hung cages in which the animal's activity shakes the cage, thus moving a pen which marks a moving paper, and (*c*) activity wheels or revolving drums.

A survey of the literature showed only one study (Babcock & Taylor, 1957) which measured motor activity of domestic fowl. These workers used a spring-hung cage. This type of cage, often, not only detects movement but disproportionately amplifies some movements and continues to resonate after the movement has stopped.

Description of the Apparatus

In an investigation of the effects of a tranquilizer on behaviour of domestic fowl, an activity cage and recording mechanism was devised and built with materials which are usually available, relatively inexpensive, and durable. Basically, the activity cage and recorder consisted of a square wire cage (for example, a poultry exhibition cage) which rested on a centre post which was several inches high. Shown in Fig. 1 is a side view of the apparatus. The present apparatus is similar in principle to an activity cage reported by Eayrs (1951) who used a cage mounted on a centre post with direct electrical contacts and a chronograph for recording activity of rats.

The cage was 24 in. × 24 in. × 26 in. and was set on a conical post $4\frac{3}{4}$ in. high. The conical post (D), which was mounted securely on a 3-ft. square of $\frac{1}{2}$ in. plywood, fits into a hole in a piece of wood which was securely attached to the floor of the cage. The hole in the wood was located in the centre of this floor. As can be seen in Fig. 1, the cage was attached to a frame 1 in. × 2 in. wood, and to this the wire and wood floor was attached as well as the eight pins and eight microswitches. One short pin (C), $\frac{3}{8}$ in. long, was placed in each corner of the base. One long pin (A), $\frac{7}{8}$ in. long, was placed halfway between the corner pins on each side. Microswitches (E) were located on both sides of each of the four long pins as shown in the insert of Fig. 1.

Movement of the animal in this cage tipped the cage, via a three point suspension system, so that it came to rest on two of the pins and the centre cone so that one of the eight microswitches mounted on the base of the cage was depressed. The switches and pins were adjusted so that only one switch could be depressed at one time. In its simplest form, the recording device involved two moderate-duty magnetic counters which were activated by the closing of any one

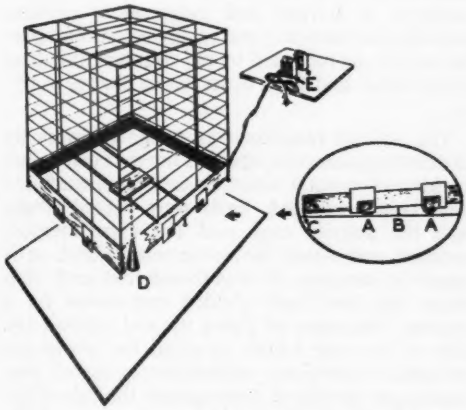

Fig. 1. Sketch of activity cage and recorder. The insert shows an enlargement of the microswitch and pin arrangement of one side. Note the microswitches (A) with a long pin (B) between them and a short pin (C) at the end. Note the placement of the centre cone (D) and the magnetic counters (E).

of the appropriately connected microswitches. For our research, two counters were used, each of which was activated by four of the eight switches, Two counters were used to preclude the possibility of an animal activating the

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switches so rapidly that the counter slipped or failed to register a second impulse occurring before the mechanism had recovered. Activation of the microswitch led the counter to advance one count. Therefore, results are reported in terms of number of counts per unit of time.

The materials used to construct one such cage were as follows: (*a*) one wire cage, 24 in. × 24 in. × 26 in., for example, wire collapsible exhibition coop; (*b*) plywood base over which the cage rests, 3 ft. × 3 ft. × ½ in.; (*c*) one solid wooden cone, 1⅝-in. base, and 4¾in. high; (*d*) wooden frame of the dimensions of the cage and a wooden centre board, 6 in. × 8 in. × ½ in. with a half-inch hole drilled in the centre of it; (*e*) eight wood screws at least 1½ in. long; (*f*) eight 110-volt microswitches; (*g*) approximately 20 ft. of bell wire; (*h*) two moderate-duty, 110-volt counters, and (*i*) approximately 8 ft. of rubber-insulated lamp wire.

Performance of the Apparatus

Three procedures were used to determine the characteristics and validity of the activity recorder. They were: (*a*) simultaneous visual check of movements of birds and counts indicated on the counter; (*b*) correlation between visual recordings of activity and independent counter recordings of activity; and (*c*) gross tests comparing activity as recorded by the counters and drug levels which had been observed to change activity.

The activity recorder was designed primarily to detect movements; thus, as the first test to get an idea of exactly what classes of movements were being recorded, birds were placed singly into the activity cage and the experimenters watched and noted the movements which activated the counters. It was found that each step which the bird took yielded one count on a counter. Instances of flying up and against the side of the cage which occurred for about ten per cent. of the birds, yielded approximately two counts per second of time against the side of the cage. A bird which paced along one side of the cage, rocked it back and forth with the long pin in the centre of that side as the fulcrum. This activated the microswitch first on one side of the long pin and then the microswitch on the other side of that pin. Activity confined to one corner of the cage, rocked the cage back and forth with the short pin at the corner as the fulcrum. This activated the microswitch on one side of the short pin and then the microswitch on the other side of the short pin. The types of responses which were not usually recorded were head movements, lifting one leg and returning it to the same place, and pecking at the floor of the cage. It was also observed that activity levels seemed to stabilise, that is, to yield constant scores in time for a bird after the first 30 to 60 minutes in the apparatus.

The second procedure used to validate the apparatus involved testing 26 mature domestic fowl individually while making a visual tally of their movements in the cage and then checking the counter readings. Each bird was placed in the cage and the counters were placed in a soundproof drawer and the experimenter tallied the bird's movements while seated approximately ten feet from the cage. Each step received one tally, while head movements, etc., were disregarded. Each bird was tested for approximately ten minutes as the upper limit of the time the experimenter could remain continuously alert.

Wide individual differences in activity levels were observed with some birds making as few as five movements and some making as many as 150 movements during the observation period. A rank order correlation coefficient was computed between the visually obtained activity scores and the counter activity scores. The calculations yielded a highly significant, positive, rank order correlation of 0·90. In addition to the fact that the two scoring systems ranked the activity levels of the birds very similarly as seen from the degree of correlation between these measures, the absolute values were also quite similar. In 62 per cent. of the cases, visual and counter scores differed by less than ten counts. At activity levels less than the mean, 100 per cent. of the cases had scores which differed by less than ten counts. The four cases in which larger discrepancies occurred were those in which high activity levels were indicated. In these instances, the experimenters felt that the bursts of activity shown by the birds were probably more accurately assessed by the counters than by the experimenter. That is, the errors were in the direction of less visual counts than counter counts, which probably was due to not seeing and thus not tallying all of the steps the birds were taking.

The effects of tranquilizers on activity levels of domestic fowl had been carefully observed and it was noted that increased drug levels led in general to decreased activity levels. Thus, as a gross test of the activity recorder, the activity levels of small groups of birds treated with

various amounts of tranquilizers were obtained using the activity cage. Activity was recorded for 30 minutes for each group and the following mean activity scores were obtained: controls 49·0 counts; lowest drug level, 38·3 counts; five-fold increase in drug level, 6·7 counts; fifty-fold increase in drug level, 0·0 counts.

The apparatus described in this paper has been in use for more than six months during which approximately 100 hours of recording have been registered and the components as described above were holding up with no replacements required. With a slight modification of the cage holding the animal, the apparatus has also been successfully used with mink and is probably suited for use with other species.

Summary

An activity cage and recorder were constructed for use with domestic fowl and small animals. The cage consisted of a square cage mounted on a centre post, pins and microswitches. Two magnetic counters, activated by the micro-switches, served as recorders. Three independent sources of observation, (*a*) simultaneous visual check of birds' movements and counter activations, (*b*) correlation between visual records and independent counter recordings (rank order correlation equals 0·90), and (*c*) activity records with increasing doses of tranquilizers, gave reason to believe that this method of recording activity was highly reliable.

Acknowledgments

The construction of a number of such activity recorders was facilitated by a grant-in-aid from the Smith, Kline & French Laboratories, Philadelphia, Pennsylvania. The grant was provided to investigate the effects of several tranquilizers on behaviour and growth of domestic fowl.

REFERENCES

Babcock, M. J. & Taylor, M. W. (1957). Effect of meprobamate on growth and feed efficiency of chickens. *Poult. Sci.* **36** (3), 485-487.

Eayrs, J. T. (1951). The activity of the female albino rat during lactation. *J. Endocr.*, **7**, 349-356.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

Abstract of a paper read at the Ordinary Meeting of 23rd September, 1958, and reported by title only in the previous issue (7, 115).

TWO ASPECTS OF THE BEHAVIOUR OF *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae)

BY C. D. PUTNAM

Department of Zoology, Cambridge

1. *Non-random behaviour by adults in a Y-maze.* Seventy-three adults of *Aleochara bilineata* each made a series of 20 choices in a Perspex Y-maze with neither reward nor punishment in either arm. Their behaviour was markedly non-random, as many of the beetles deviated significantly from equal choice of the two alternatives, i.e. chose one alternative fifteen or more times out of twenty; 58·91 per cent. of the beetles did so, whereas if they had chosen at random only 4.14 per cent. would have done so. On any occasion the beetles tended to choose the same alternative as that chosen previously. On the second choice 71·24 per cent. of the beetles chose the alternative they chose the first time (cf. 50 per cent. expected if choices at random), 78·8 per cent. of those which had chosen the same alternative twice chose the same one on their third choice, and of these 82·9 per cent. chose the same one again on their fourth choice. However, after from one to four choices of one alternative and then one choice of the other, beetles showed no preference for either on their next choice. 29 beetles each made two series of twenty choices in the Y-maze, from a few hours to thirteen days apart, and tended to show either a significant preference for the same alternative, or no preference for either, in both series.

It is thought that the beetles made their first choice in the maze at random, and then developed a preference for one alternative as the result of learning, although there was no difference between the alternatives. It seems possible that learning could occur under these circumstances, if escape from the end of the arm acted as a reward, and if the beetles were not aware when they chose that choice of either alternative would have the same result.

2. *Host-finding and selection by the first-instar larvae.* The females of *A. bilineata* lay their eggs in the soil, and the first-instar larvae, 1½-2 mm. long, have to find suitable puparium of the host, *Erioischia brassicae* Bche. (Diptera: Anthomyiidae), in which to complete their development. The behaviour of these larvae was studied under experimental conditions. Host-finding movements were apparently random in the sense that they were not directed by stimuli from the hosts. In a universe with equal numbers of unsuitable puparia (*Calliphora*) and *E. brassicae* puparia the two types of puparia were not attacked equally often, the former only being attacked very rarely; the larvae also avoided attacking puparia already attacked by their own species. Thus they could distinguish unsuitable hosts, and, to a large extent, refrain from attacking them. Such host-finding and selection behaviour is not unusual in insect parasitoids, but it has not been previously recorded for a larval parasitoid.

Paper read at the Ordinary Meeting of the Association for the Study of Animal Behaviour at Birkbeck College, 9th January, 1959.

IN PRAISE OF ANTHROPOMORPHISM

BY C. W. HUME

U.F.A.W., London

The subjective experiences of brutes may be conceived of by analogy with human subjective experiences. This practice, known as "anthropomorphism," is out of fashion in consequence of its having been used incautiously, and words like "hunger" and "fear" are often written with

quotes when they refer to brutes. Thus what began as scientific criticism has degenerated into quasi-philosophic pedantry. A judicious practice of anthropomorphism is justified by (1) the intuitive interpretation of behaviour, which resembles the intuitive interpretation of human facial expression; (2) experience of animal-trainers and the like; (3) the theory of evolution; (4) responses to traumatic stimuli; (5) homology and analogy of the nervous system of men and brutes; (6) flexibility of instinctive patterns of behaviour; (7) rudimentary language; (8) electroencephalography; (9) learning by rewards and punishments.

One argument against anthropomorphism is the same as that used by anti-vivisectionists against medical research, and relies on the differences between species. It appears to depend on a confusion of conceptual thinking with mental imagery. Descartes's views on animal automats were opposed by John Ray, John Locke, David Hume, Charles Darwin, J. G. Romanes; but Lloyd Morgan's canon then imported a systematic mechanistic bias.

The second argument is the positivist or objectivist, but when this passes from a method into a dogma it leads to solipsism. Its history illustrated by reference to Pyrrho of Ellis, William of Ockham, Auguste Comte, and J. B. Watson. On the other hand, W. H. Thorpe and the Lorenz-Tinbergen school find a place, along with objectivist methods, for subjective insight into behaviour. The reply to solipsism and anti-anthropomorphism.

PROCEEDINGS OF THE SECTION OF ANIMAL BEHAVIOR AND SOCIOBIOLOGY (ECOLOGICAL SOCIETY OF AMERICA AND THE AMERICAN SOCIETY OF ZOOLOGISTS)

The following papers were read at the Annual Meeting, 31st August to 2nd September, 1959.

THE PHYSIOLOGY AND BIOCHEMISTRY OF BEHAVIOUR

C. C. CARPENTER, presiding.

POLYPHENOLS AND BEHAVIOUR OF THE AMERICAN COCKROACH By THOMAS SMYTH Jr., *The Pennsylvania State University.*

FEEDING BEHAVIOUR OF *Verrucosid* AMOEBAS. By EUGENE C. BOVEE, *University of Florida.*

HYDROSTATIC BALANCE IN *Xenopus* LARVAE. By WILLEM A. van BERGEIJK, *Bell Telephone Laboratories.*

EFFECTS OF SPECIFIC SUBTOTAL LABYRINTHECTOMY OF THE RIGHT LATERAL SEMICIRCULAR CANAL IN THE KANGAROO RAT (*Dipodomys*). By ROBERT D. BURNS, *Oklahoma University*, and THOMAS W. JENKINS, *Michigan State University.*

THE RELATIONSHIP OF TESTICULAR CHOLESTEROL TO HORMONAL ACTIVITY AND BEHAVIOUR IN THE STARLING. By F. K. HILTON, *School of Medicine, University of Louisville.*

EOSINOPHIL RESPONSE TO AGGRESSIVE BEHAVIOUR IN CFW ALBINO MICE. By JOHN G. VANDENBERGH, *Ohio University.*

BEHAVIOURAL AND ENDOCRINE RESPONSE OF MICE, RATS AND GUINEA PIGS TO INTENSE NOISE STIMULATION. By ADAM ANTHONY, EUGENE ACKERMAN and JAMES LLOYD, *The Pennsylvania State University.*

SEX DIFFERENCES IN AUDIOGENIC SEIZURE SUSCEPTIBILITY. By JACK WERBOFF and JOHN CORCORAN, *Lafayette Clinic and Wayne State University.*

LEARNING AND SOCIOBIOLOGY

H. E. WINN, presiding.

THE EFFECT OF "WILDNESS" ON LEARNING IN THE WYOMING GROUND SQUIRREL. By R. H. DENNISTON, *University of Wyoming.*

GROWTH RETARDATION IN GOATS DURING PERIODS OF CONDITIONED REFLEX TRAINING. By ULRIC MOORE, *Behaviour Farm Laboratory, Cornell University.*

THE ROLE OF IMITATION IN FOOD-DISCRIMINATION BY BIRDS. By PETER H. KLOPFER, *Duke University.*

IMPRINTING WITH VISUAL FLICKER; EVIDENCE FOR A CRITICAL PERIOD. By H. JAMES, *Queen's University, Kingston, Ontario.*

RECENT FINDINGS IN PIGEON ORIENTATION. By K. SCHMIDT-KOENIG, *Max Planck Institute, Germany.*

DEPTH PERCEPTION IN LAMBS AND KIDS. By JALAL BESHARAT, JOHN WILEY, ULRIC MOORE, *Behaviour Farm Laboratory, Cornell University.*

NURSING-SUCKLING INTERACTIONS IN THE DOMESTIC PIG. By E. S. E. HAFEZ, *State College of Washington, Pullman, Washington.*

THE INFLUENCE OF A DIFFERENCE IN SPECIES BETWEEN MOTHER AND YOUNG ON THE PROTECTION AND VITALITY OF THE OFFSPRING. By HELEN BLAUVELT, JULIUS B. RICHMOND and ULRIC MOORE, *Behaviour Farm Laboratory, Cornell University.*

MIXED COLONIES IN ANTS. By R. L. KING, *Iowa Lakeside Laboratory, State University of Iowa,* and R. M. SALLEE *Western Illinois University.*

THE GENETICS OF BEHAVIOUR AND SEXUAL BEHAVIOUR

E. B. HALE, presiding.

A COMPARISON OF TWO SUBSPECIES OF *Peromyscus maniculatus* AT WEANING. BY JOHN A. KING AND JOHN C. DESHAIES, *Roscoe B. Jackson Memorial Laboratory.*

NEST MATERIAL CARRYING BEHAVIOUR OF F_1 HYBRIDS BETWEEN *Agapornis fischeri* AND *A. roseicollis.* BY WILLIAM C. DILGER, *Cornell University.*

INHERITANCE OF SEASONAL BREEDING BEHAVIOUR IN THE BASENJI (AFRICAN BARKLESS) DOG. BY J. P. SCOTT AND J. L. FULLER, *Roscoe B. Jackson Memorial Laboratory.*

GENETIC DIFFERENCES IN THE REPRODUCTIVE BEHAVIOUR OF DOMESTIC COCKERELS. BY D. G. M. WOOD-GUSH, *A.R.C. Poultry Research Centre, Edinburgh, Scotland.*

THE EFFECTS OF DIFFERENT EXPERIMENTAL SITUATIONS ON SEXUAL BEHAVIOUR IN CHICKENS. BY A. M. GUHL, *Kansas State University.*

AN HYPOTHETICAL MODEL CLARIFYING THE EFFECT OF EARLY SOCIAL EXPERIENCE ON SEXUAL BEHAVIOUR. BY M. W. SCHEIN AND E. B. HALE, *The Pennsylvania State University.*

QUANTITATIVE MEASUREMENTS OF THE DISPLAY BEHAVIOUR OF THE GOLDENEYE *(Bucephala clangula).* BY BENJAMIN DANE, CHARLES WALCOTT AND WILLIAM H. DRURY, JR., *Harvard University, Cornell University.*

SEXUAL REACTIONS OF MALE TURKEYS TO DEVIATIONS FROM A NORMAL FEMALE HEAD MODEL. BY H. E. T. SCHOETTLE AND M. W. SCHEIN, *The Pennsylvania State University.*

STIMULI TERMINATING SEXUAL RECEPTIVITY IN FEMALE TURKEYS. BY E. B. HALE, *The Pennsylvania State University.*

SOCIAL BEHAVIOUR

J. A. KING, presiding.

FEEDING ADAPTATIONS AND BEHAVIOUR OF A FRESHWATER DOLPHIN, *Inia geoffrensis.* BY JAMES N. LAYNE, *University of Florida.*

TIME AND MOTION STUDY OF PREFIGHTING BEHAVIOUR IN MICE. BY EDWIN M. BANKS, *University of Illinois.*

AGONISTIC BEHAVIOUR AND TERRITORY IN THE AMERICAN REDSTART, *Setophoga ruticilla.* BY MILLICENT S. FICKEN, *Cornell University.*

SOCIAL FACTORS INFLUENCING SPATIAL DISTRIBUTION IN POPULATIONS OF PRAIRIE DEER MICE. BY C. RICHARD TERMAN, *Roscoe B. Jackson Laboratory and Zoology Dept., Michigan State University.*

EFFECT OF VISUAL AND VOCAL STIMULATION ON BREEDING IN THE BUDGERIGAR *(Melopsittacus undulatus).* BY ROBERT W. FICKEN, MILLICENT S. FICKEN, FRED SIBLEY AND ARI VAN TIENHOVEN, *Cornell University.*

BEHAVIOUR OBSERVATIONS ON THE PRAIRIE DOG. BY DARHL FOREMAN, *Western Reserve University.*

SOME ASPECTS OF SOCIAL ORGANISATION IN THE CAROLINA CHICKADEE. BY KEITH L. DIXON, *Hastings Natural History Reservation.*

SOCIAL ORGANISATION IN A REFUGE POPULATION OF WHITE-TAILED DEER. BY G. GENE MONTGOMERY, *Pennsylvania State University.*

BEHAVIOUR PATTERNS OF JUVENILE YELLOW-BELLIED MARMOTS *(Marmota flaviventris nosophora* HOWELL). BY KENNETH B. ARMITAGE, *University of Kansas, Lawrence.*

BEHAVIOUR STUDIES OF THE EASTERN CROW. BY GEORGE B. HAPP, *The Principia College.*

RECENT DEVELOPMENTS IN RESEARCH IN THE BEHAVIOUR OF FISHES

L. R. ARONSON, presiding.

RECENT STUDIES OF SOCIAL BEHAVIOUR IN FISHES. By BERNARD S. GREENBERG, *Roosevelt University.*

ECOLOGICAL FACTORS IN REPRODUCTIVE BEHAVIOUR OF FISHES. By HOWARD E. WINN, *University of Maryland.*

REPRODUCTIVE BEHAVIOUR IN HERMAPHRODITIC FISHES. By EUGENIE CLARK, *Cape Haze Marine Laboratory.*

MORPHOLOGIC SPECIALISATIONS AND REPRODUCTIVE BEHAVIOUR. By ARLENE TUCKER, *Rutgers University.*

OBSERVATIONS ON PREDATOR-PREY RELATIONSHIPS IN FISHES. By F. G. WOOD, *Marine Studios.*

PSYCHOPHARMACOLOGIC DRUGS AND FISH BEHAVIOUR. By JAMES W. ATZ, *New York Aquarium, New York Zoological Society, New York.*

PROBLEMS OF STRESS IN FISH BEHAVIOUR. By JAMES W. ATZ, *New York Aquarium, New York Zoological Society, New York.*

DISEASES AND FISH BEHAVIOUR. By ROSS F. NIGRELLI, *New York Aquarium.*

SOME EXPERIMENTS ON LEARNING ON *Tilapia.* By M. E. BITTERMAN and JEROME WODINSKY, *Department of Psychology, Bryn Mawr College.*

BASIC PRINCIPLES OF SUN ORIENTATION IN FISHES. By WOLFGANG BRAEMAR and HORST O. SCHWASSMANN, *University of Wisconsin.*

THE USE OF UNDERWATER TELEVISION FOR STUDYING THE BEHAVIOUR OF MARINE FISH IN TRAWL NETS. By ROBERT LIVINGSTONE, Jr., *Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Massachusetts.*

OBSERVATIONS ON THE BEHAVIOUR OF HERRING IN CURRENTS USING UNDERWATER TELEVISION. By VIVIEN M. BRAWN, *Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.*

APPLICATION OF BEHAVIOURAL INVESTIGATIONS TO FISHERIES PROBLEMS. By ALFRED PERLMUTTER, *New York University.*

FISH BEHAVIOUR AND FISHWAYS. By GERALD B. COLLINS.

BOOK REVIEWS

Bumblebees. By J. B. FREE & C. G. BUTLER. London: Collins, 1959. Pp. 208. 25s.

This book provides a useful introduction to bumblebees. The text is mostly compiled from scientifically published observations. References are given, with titles, in an extensive bibliography, and there is a good index. In appendices by Dr. Ian Yarrow there are keys to the identification of British bumblebees, and an account of the distribution of the British species.

Although the statements in the book are documented and the bibliography is extensive, the book is not a review in the scientific sense. The quoted examples are not necessarily the earliest or the only examples of the behaviour described (e.g. quarrels among egg-laying workers, see Sladen, 1912, p. 53 and 241). The authors' views are given in full, but they are not always contrasted with contrary views held by others; for instance, the experiments of Free (1955) are quoted in the chapter on division of labour, and a reference is given to the work of Brian (1952), but the fact that Brian obtained opposite results and drew contrary conclusions is not mentioned.

Throughout the book the emphasis is on description, not on analysis. This attitude makes the book more palatable than it otherwise would be to the general reader, for whom this series of books is produced.

Dr. Colin Butler has decorated the book with 24 pages of attractive black-and-white photographs, and as a frontispiece there is a colour plate of some of our common bumblebees, which will be of help to those who are commencing to study them.

C.R.R.

Fundamentals of Ornithology. By J. VAN TYNE & A. J. BERGER. London: Chapman & Hall. 1959. Pp. 624. 94s.

The way in which this work came to be completed some twelve years after the death of the senior author is described graphically in the preface. As originally planned, the book was to comprise 21 chapters, of which 13 only have in fact been included. "It soon became evident, however, that the cost of publishing such a book would be prohibitive. Thus, instead of receiving full chapter treatment, some important subjects (e.g. physiology, genetics, ecology, study methods) had to be mentioned very briefly where pertinent in several chapters, and still other subjects (conservation, game arrangement, population dynamics, museum techniques) not at all." It may be assumed that similar considerations of space have precluded any attempt to supply lists of species against the chapter on "The Classification of World Birds by Families" that, we are told, the senior author had considered to be the real basis of the book.

Fundamentals of Ornithology is stated to be for the student who has already become well grounded in the several basic branches of biology before specialising in ornithology. It has nevertheless been felt desirable to incorporate a glossary, occupying nearly 30 pages, which includes many terms that are in wide biological use as well as specialised ornithological definitions.

Berger is to be congratulated on the obvious zeal and care with which he has strived to complete this work according to the senior author's plan. The twelve chapters, other than that already mentioned, deal respectively with palaeontology, anatomy, plumage and moult, senses and behaviour, voice and sound production, bird distribution, migration, flight, food and feeding habits, breeding behaviour, social relations, and taxonomy and nomenclature, and in addition to the detailed references in each of them there is a section entitled "Ornithological Sources." Literature citation on the whole seems to be well balanced and to draw freely from non-American as well as American sources. It appears to include publications up to 1956, although Marler's paper on the behaviour of the chaffinch, published in that year, is not mentioned.

The chapter on senses and behaviour draws heavily on Thorpe's *Learning and Instinct in Animals*, but is, with the chapter on breeding behaviour, clearly set out and well documented. The absence of a chapter on physiology is to be regretted, and indeed the material that had to be omitted from this work would surely constitute a valuable second volume.

A.N.W.

Practical Animal Ecology. By W. H. DOWDESWELL. London: Methuen. 1959. Pp. 315. 32s. 6d.

"An argument advanced against the introduction of ecology into the biology course at schools is that the essential preliminaries consume an inordinate amount of time." About half of this book forms a compendium of simple but

effective apparatus and techniques which surely serve to refute the above observation. Designed for sixth-form and first-year University students, as companion to the author's earlier "Animal Ecology", it offers stimulating approaches to terrestrial, fresh-water, edaphic and sea-shore habitats. Ethological studies, particularly of territorial behaviour, are stressed as a necessary adjunct to Yapp's capture-release theory and the line-transect theory for moving animals due to Fisher.

Laudably, no attempt is made to provide classificatory data, an excellent bibliography giving the necessary references to systematics. A section on elementary statistics is lucid enough to obviate the dangers inherent in a little knowledge. Probably more attention might have been profitably granted to protozoan communities, and no treatment of parasitic habitats is given. However, these minor points detract little from this broad but sound introduction to ecological method, which includes a number of ideas likely to be of use to the ethologist working in the field.

G.H.W.

With reference to the review published on p. 116 of our issue of January-April, 1959, relating to the *U.F.A.W. Handbook on the Care and Management of Laboratory Animals* by Alastair N. Worden and W. Lane-Petter, the publishers have requested that we draw attention to the fact that the binding is now completely satisfactory. Some of the early review copies were unsatisfactorily bound, but these were subsequently called in for rebinding.

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